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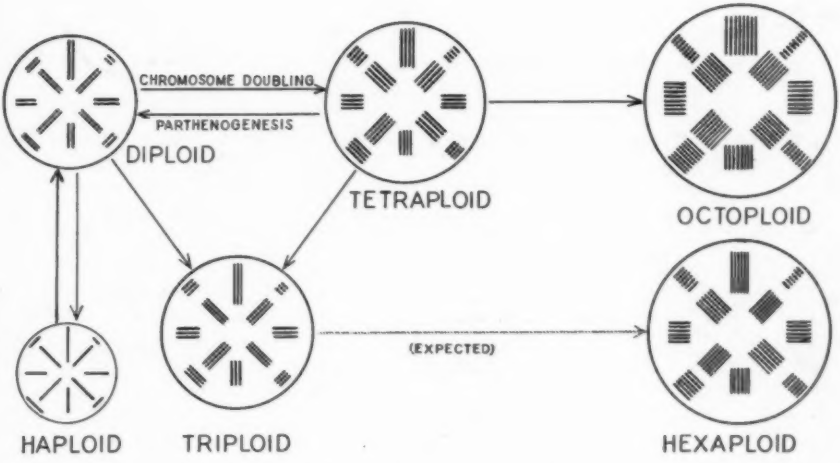

A 'PLOID PEDIGREE

(Showing Types of Polyploids Induced by Colchicine Treatment

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The JOURNAL of HEREDITY is published monthly by the AMERICAN GENETIC ASSOCIATION at 32nd Street and Elm Avenue, Baltimore, Md., and Victor Building, Washington, D. C. Address all communications regarding editorial matters to Room 308, Victor Building, Washington, D. C. Communications regarding the business management of The JOURNAL OF HEREDITY may be addressed to the publication office, 32nd Street and Elm Avenue, Baltimore, Md., or to the Victor Building, Washington, D. C. Entered as second-class matter February 24, 1923, at the postoffice at Baltimore, Maryland. Acceptance for mailing at the special rate of postage provided for in section 1163, Act of October 3, 1917, authorized December 20, 1918.

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The

Journal of Heredity

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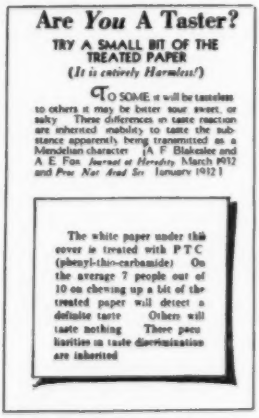
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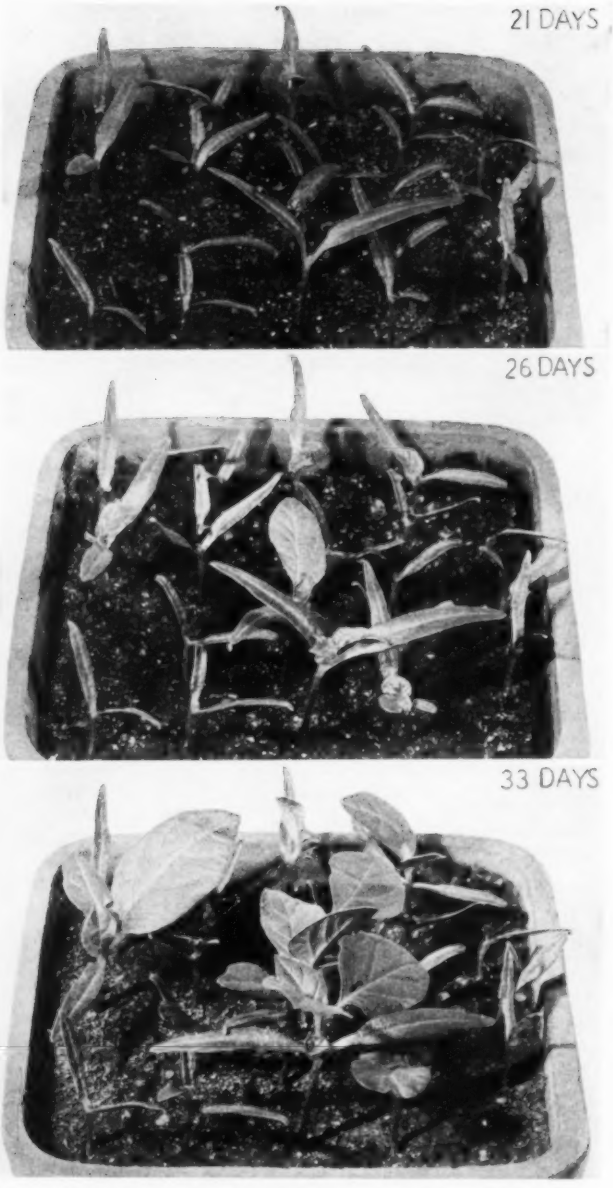


COLCHICINE-TREATED SEEDLINGS DIFFERENTIALLY AFFECTED

Frontispiece

Seedlings from seed treated with 0.4 per cent colchicine for four days, photographed at 21, 26, and 33 days after planting. All seedlings are checked in growth and some of the blind seedlings do not develop beyond the colyledon stage. Colchicine treated plants are not at once giants. They are dwarfed and deformed, and the effects of chromosome doubling may appear only in the next generation.

METHODS OF INDUCING DOUBLING OF CHROMOSOMES IN PLANTS

By Treatment With Colchicine*

ALBERT F. BLAKESLEE and AMOS G. AVERY
Carnegie Institution of Washington, Department of Genetics, Cold Spring Harbor, N. Y.

PLANTS with doubled chromosome number have occasionally appeared spontaneously in experimental cultures and have been found, though rarely, in nature. There has been considerable difference of opinion regarding the part of the plant in which the doubling has taken place. Some have expressed the belief that a tetraploid ($4n$) comes from the union of an unreduced $2n$ egg with an unreduced $2n$ sperm brought in by the pollen. The following facts furnish strong evidence that this is not the method in *Datura*. In several instances it has been possible to prove genetically that the tetraploid has come from a reduced $1n$ gamete.[9] Tetraploids in the offspring of normal $2n$ parents which are heterozygous for a given gene a should have the constitution A_2a_2 if they arose from union of unreduced gametes. When they do not have this constitution, as often has been the case, previous reduction must have taken place. Buchholz[11] has shown that the $2n$ pollen tubes from a tetraploid regularly burst when growing in the style of a diploid and hence the $2n$ pollen grains which are occasionally formed by normal plants through non-reduction could not be expected to take part in the production of tetraploid seedlings.

That the doubling of chromosomes occurs in somatic tissue after the formation of the first cell of the embryo is evident from the peculiarities of plants which have arisen as chromosomal mutations in our cultures. Of these we have recorded several hundred. In some cases the doubling has occurred as a sectorial chimera of $4n$ tissue on an otherwise $2n$ plant.[7,8] Frequently the whole plant appears involved. Almost always it is at first malformed in growth with characteristically thick and roughened leaves, due to the different growth-rates of the $2n$ and $4n$ tissue. These we have learned to recognize as "mixochimeras" with $2n$ and $4n$ tissue and have been in the habit of recording them as "rough tetraploids." The first tetraploid recorded for *Datura* was discovered in 1916. A photograph of this plant published in the *Journal of Heredity*[6] shows one half with only rough leaves and the other half with a high proportion of smooth, broad leaves with which we have become familiar as characteristic of tetraploid races. Spontaneous tetraploids have frequently been recognized at an early stage from the swollen condition of the stem below the cotyledons and have been marked for selection while still in the seed pan. Chromosome counts have demonstrated that $4n$ and $2n$ cells may be present together in the same flower and even in the same anther of spontaneous or induced "rough tetraploids" and the same flower may have pollen grains of two sizes, $1n$ and $2n$. Extensive checks with chromosome counts have shown that size of pollen grains is an adequate

*The present article is a report of a paper presented at the recent Rochester meeting of the National Academy of Sciences, of which an abstract has been published in Science.[4] An earlier account of the doubling of chromosomes by use of colchicine was presented this last August at the Woods Hole meeting of the Genetics Society of America. A preliminary report was published in the *Comptes Rendus*.[3]

GROWTH RETARDED BY COLCHICINE

Figure 1

Seedlings of *Datura stramonium*, 15 days from planting. Control on left. Seedlings on right came from seeds treated with 0.4 per cent colchicine for one day. Note relatively slow growth of treated seedlings.

criterion whereby a tetraploid can be distinguished from a diploid.

Doubling the number of chromosomes in cells of roots seems to be a relatively common phenomenon. In the classical experiments of Nemec, first reported in 1904, the doubling was induced by treatment with chloral hydrate and other narcotics, but in many cases roots with tetraploid tissue have appeared without known stimuli. It has not seemed possible heretofore to extend the method of Nemec with roots to the induction of tetraploidy in stems. It is the latter alone, however, which are of interest to the plant breeder since they involve the flowers and hence can give rise to 4*n* races. Several years ago the senior author attempted to induce tetraploidy by injecting chloral hydrate into the developing ovary. Gene mutations and chromosome deficiencies were apparently induced by the treatment, but no doubling of chromosomes was secured. Attempts were earlier made to obtain chromosomal types by means of cold treatment.[10] The cold resulted in the production of aborted pollen and an abundance of large pollen grains of the size formed by tetraploids, but there was no evidence that the treatment had stimulated the production of tetraploids in the offspring.

The fact that in certain seasons we have had a relatively large number of tetraploids in our garden cultures, but in other seasons few or none, and the added fact that seed from a given envelope might produce many 4*n* plants in a high tetraploid season and none in a poor tetraploid season, indicated that environmental factors were involved. High temperatures to which the seed pans were sometimes subjected during germination were suggested as a possible stimulus. However, a considerable number of tests with high temperatures during germination, both continuously and intermittently applied, failed to bring out tetraploids. Randolph,[14] however, has been successful in the application of heat to early cells of the developing embryo of maize. By his methods he has succeeded in getting a maximum of around 5 per cent of the embryos treated to develop into tetraploids. Although this method of inducing tetraploids has been the most successful up to the present time, it apparently requires rather careful control of the experimental conditions and seems not to be of general application.

More recent experience with induction of mutations in *Datura* by treatment with radium, x-rays, heat, and aging of seeds has shown that the seed is a most convenient part of the plant in which to

COLCHICINE-TREATED PLANTS ARE VARIOUSLY DEFORMED

Figure 2

A—Normal (2*n*) control plant and a strongly affected rough-leaved plant which produced a 4*n* flower. The seed from which this plant came as well as the two plants shown below (*B*), had been soaked in a 0.2 per cent solution of colchicine for ten days. *B*—The plant on the left shows a vigorous branch which bore flowers with giant pollen grains of a size characteristic of 4*n* tissue. One of its flowers had 20 per cent of super-giant pollen grains which must have come from 8*n* tissue. Plant on right had thrown out a vigorous branch which, from the size of its pollen grains, was shown to be 2*n*. The confused growth at the base undoubtedly contained some 4*n* tissue which might have been forced into flower if the 2*n* branch had been cut off. *C*—A triploid (3*n*) plant which had been sprayed (see Figure 5*D*) with the hope of inducing doubling of chromosomes to form a 6*n* or hexaploid plant. Older leaves are unaffected. Leaves that were wetted only on upper surfaces are strongly buckled downward by abnormal growth. Leaves which were in bud at time of treatment are dwarfed and strongly roughened. *D*—Two plants which had previously been treated with agar solutions of colchicine following the method shown in Figure 5*B*. The treated leaves of both are roughened in a manner characteristic of tissue from spontaneous tetraploids. The flowers of both had different proportions of giant pollen grains which showed that they had originated from 4*n* tissue.

obtain mutations, but with none of these treatments have we been able to induce tetraploidy.

Since we had learned the value of the seed in the induction of mutations, a new attempt was made this last June to induce doubling of chromosomes by chemical treatment. Chloral hydrate, which was one of the several narcotics tested, inhibited germination in a concentration of 6.4 per cent when seeds were immersed in it for ten days. A 3.2 per cent solution and several weaker concentrations caused the seedlings to come up without purple pigment, which was only slowly regained. None of the chemicals so far tested, however, induced any indications of tetraploidy except colchicine.* As soon as the seed which had been treated with this alkaloid germinated, the swollen hypocotyls of the seedlings at once led us to believe we had at last

*For inclusion of colchicine among the chemicals tested, the senior author is indebted to the suggestion of Dr. O. J. Eigsti, then an assistant in the Department of Genetics, who had observed polyploid cells in roots after treatment with colchicine.

CHIMERAL GROWTH CAUSED BY COLCHICINE TREATMENT

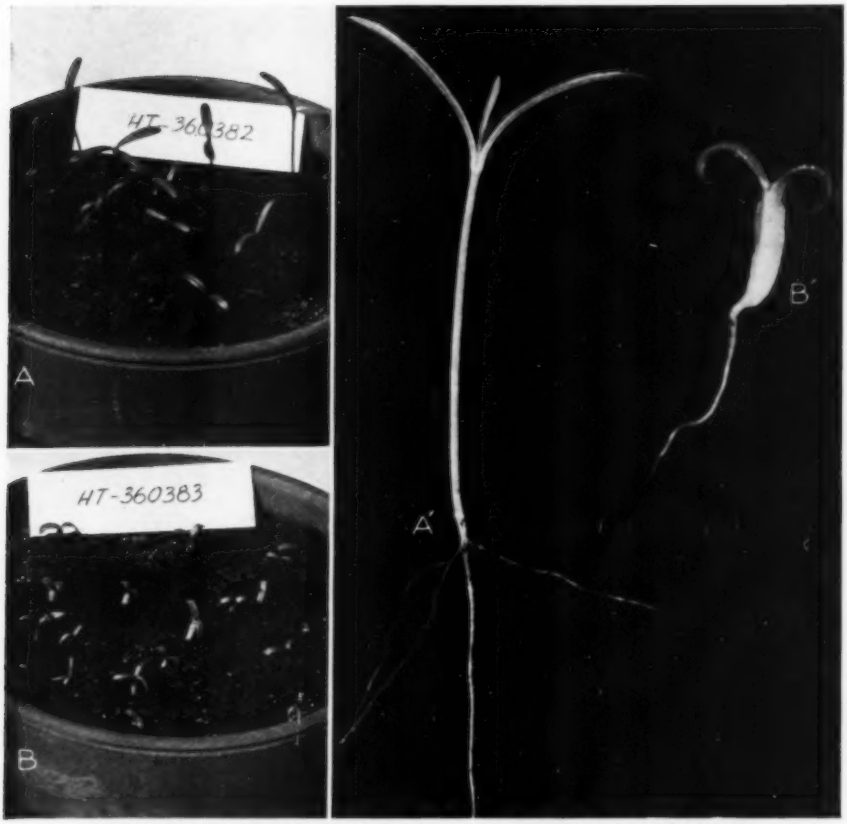
Figure 3

A—Plant from seed treated with 0.8 per cent colchicine showing a clean 4*n* leaf and other leaves with rough tissue. *B*—Plant from seed treated with 0.2 per cent, showing a clean 4*n* branch and a branch with all the leaves roughened due to their containing diploid and tetraploid tissue. *C*—Plant from seed treated with 0.2 per cent colchicine. It had all pollen of the size characteristic of 4*n* tissue. In appearance it would pass for a clean tetraploid if it did not have the malformed leaf at base.

found a method of inducing an abundant production of tetraploids. This belief was strengthened when the plants began to show the characteristically roughened leaves which we had come to associate with spontaneous tetraploids. Final proof came with determination of size of pollen grains and chromosome counts and with recovery of tetraploids in the second generation. When seeds are heavily treated, plumule growth is checked, shoots develop from axils of cotyledons, and buds are abnormally arranged. Sometimes even the buds in axils of cotyledons are inhibited and no growth takes place beyond the cotyledon stage. Following the treatment with colchicine, there are formed sectors with roughened leaves characteristic of mixed 4*n* and 2*n* tissue like that of spontaneous 4*n* mutants. It has been earlier shown for *Datura*[12] that when a seed is treated with a given stimulus, only part of the initial cells which develop into the shoot undergo mutation. In consequence, these mutated cells give rise to mutated sectors in the adult plant. Smooth-leaved 4*n* tissue and especially normal 2*n* tissue tend to outgrow the mixture of 4*n* and 2*n* cells. Tetraploid tissue involving the flower may readily be determined by examination of pollen.

Treatment of seeds is probably the most satisfactory method of using colchicine for the induction of tetraploids in *Datura*, although other parts of the plant have been successfully treated by methods which will be described later.

With *Datura*, soaking seeds in tap water solutions for varying lengths of time up to two weeks has been effective. With seeds of certain other species, however, immersion for any considerable time hinders germination and in such cases seeds have been laid on a moist substratum with exposure to air for a short time to start early stages of germination before treatment with the colchicine. The immediate effect of treatment is a general retardation of development seen in the slow germination and growth of seedlings even when the doses are too weak to bring about visible changes in the adult plants. This difference is evident



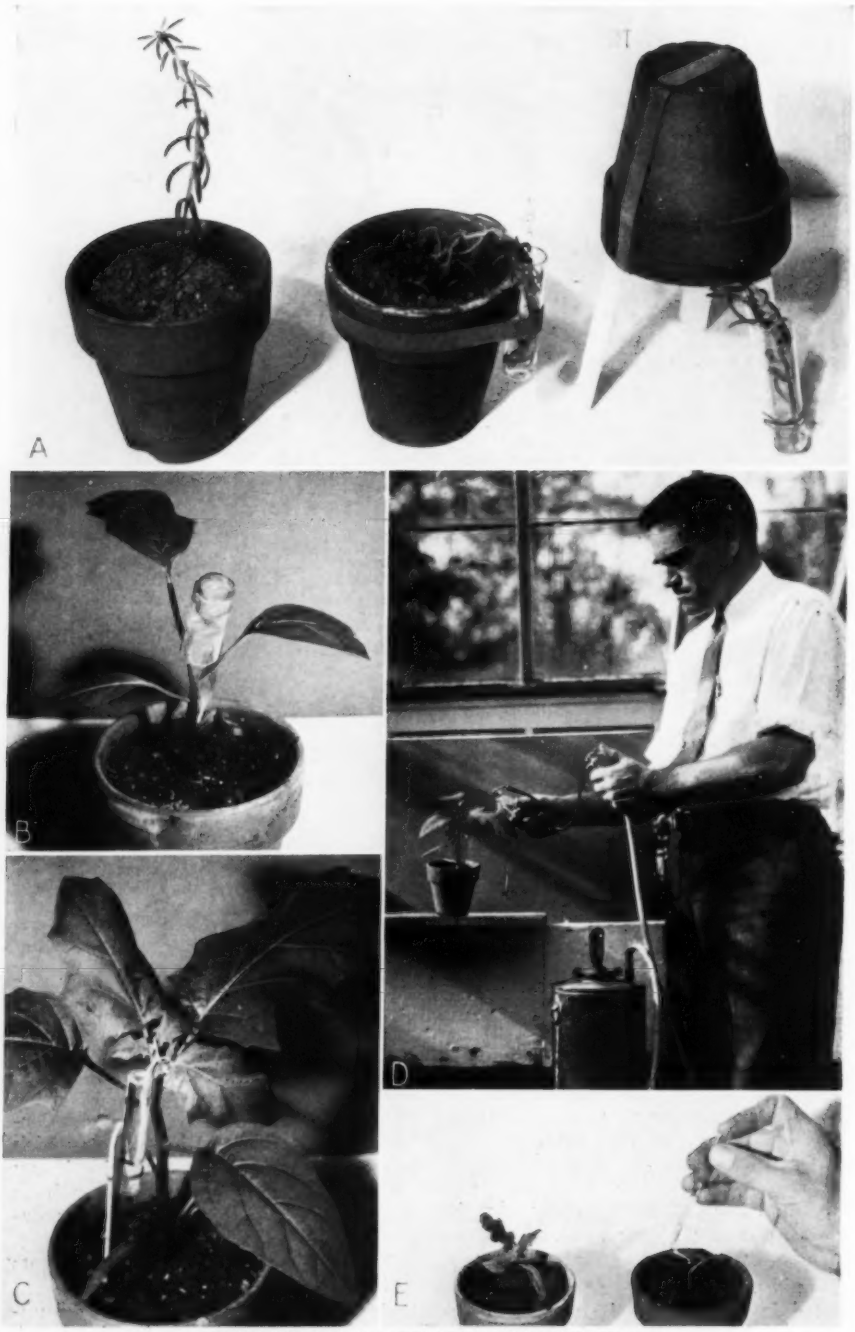
DEFORMITY RESULTING FROM COLCHICINE TREATMENT

Figure 4

Seedlings of *Cosmos* photographed about two weeks from planting. A-A′ show seedlings of untreated controls; B-B′ show seedlings from seeds treated for four days with 0.05 per cent colchicine. Seedlings from treated seeds have swollen stems and poor root development. In consequence, they are often washed out of the soil when the seed pan is watered because of lack of root anchorage. It is these dwarfed and malformed seedlings which produce the tetraploid tissue which in the next generation may give rise to pure-breeding polyploid species due to their containing both diploid and tetraploid tissue.

in Figure 1, in which the pan on right came from seed treated with 0.4 per cent colchicine for one day. The right hand pan seems to be slightly checked in plumule development in comparison with the control on left. The two pans were photographed 13 days after planting. However, only three out of 21 plants tested from the treated pan had ± 4*n* flowers. The seedling at the lower right of the pan appears to be nearly blind, as also one at the upper left corner. Perhaps these were two of the three which later showed 4*n* tissue. Following heavy treatment, the checking of growth is more marked and recovery longer delayed, as shown in Frontispiece.

Figures 2*A-B* and 3 show potted plants which have been affected by treatment with colchicine compared with an untreated control on the left in Figure 2*A*. The plant on the right in Figure 2*A* has



METHODS OF APPLYING COLCHICINE

Figure 5

A—Portulaca plants showing method of treating stems by immersing their tips in solutions of colchicine. Such treatment has induced doubling of chromosomes. *B*—A successful method of inducing chromosome doubling by covering the tip of a *Datura* plant with an agar solution

the broad, roughened leaves typical of "rough tetraploids." It produced a flower with pollen of the size characteristic of $4n$ tissue. The plant on the left in Figure 2*B* shows a vigorous branch which has grown out from the confused tissue. It had flowers with pollen of the size from $4n$ tissue. In one flower there were 20 per cent super-giant pollen grains which indicated that they had come from octoploid or $8n$ tissue. The branch which had grown out of the confused base of the plant at right in Figure 2*B* was shown to be normal diploid ($2n$) by the size of pollen. In Figure 3 the plant at left (*A*) shows a smooth $4n$ leaf in contrast to the others which are more or less roughened. It produced $4n$ flowers, as shown by pollen size. The plant on the right (*B*) has a smooth-leaved $4n$ branch in the process of outgrowing the rough-leaved branch which was apparently earlier in development. By the pollen test this branch was shown to be $4n$. Figure 3*C* shows a plant which could be taken as a typical representative ot a tetraploid race were it not for the abnormal leaf at the base. A clean $4n$ branch had grown out from the early confused tissue and produced $4n$ flowers with large pollen grains.

Concentrations

Treatment of seeds with colchicine within a wide range of concentrations is effective in inducing branches with doubled chromosome number. Table I shows results with concentrations varying from 0.003125 per cent to 1.6 per cent. For each treatment, 25 seeds were used. The plants were classified first by appearance into those entirely normal $2n$ and those $\pm$ $4n$, i.e., those which showed external evidence of having some $4n$ tissue. Later the same plants, as many as had flowered, were reclassified by pollen size. Only records of at least 10 per cent of a given type of pollen are considered in the table. Some of those most heavily treated had died in the seedling cotyledon stage before records were taken. One each from the cultures No. 3601029 and No. 3601031 were rough, confused in growth, and almost blind so that if flowers should succeed in forming they would be expected to be at least $4n$ or $4n + 8n$. None of the ten-day treatments below 0.1 per cent gave any evidence of being effective. Treatment with 0.1 per cent showed less than ten per cent of the plants with external evidence of tetraploidy and none showed $4n$ flowers. From 0.2 to 1.6 per cent the number of plants with $4n$ appearance, as well as those which produced $4n$ flowers, averages over 50 per cent. If it had been worth while to do so, it probably would have been a simple matter to have debudded branches that appeared normal $2n$ and to have favored those that appeared $4n$ and thus to have obtained a proportion of $4n$ flowers considerably higher than that recorded in the table. The right hand plant in Figure 2*B* would have been a favorable plant for such operative procedure.

In another series of *Datura* seeds, treatments with 0.2 per cent solutions were given to ten seeds for 6 hours, 12 hours, 24 hours, 2 days, and 4 days. From this series none of the seedlings was recorded as $\pm$ $4n$ except in the 4 days' treatment in which 6 out of 10 were listed as tetraploid by inspection and 4 out of 9 had $4n$ flowers. The treatment for one day gave a single plant with a flower in which 10 per cent of the pollen was of the size expected from $4n$ tissue. With this partial exception, the series indicates that treatment of *Datura* seeds for less than 4 days with 0.2 per cent solutions would have little

LEGEND TO FIGURE 5—CONTINUED

of colchicine. *C*—Capillary string method of treating buds with solutions of colchicine. One end of string is immersed in a bottle of solution and the other end is wrapped around buds to be treated. *D*—Method of applying spray of colchicine solutions by means of an atomizer with air pressure furnished by a spray tank. The air pressure valve manipulated with the left hand was obtained from a dental supply house. *E*—Drop method of treatment. On right a drop of solution is being applied to a seedling *Datura*. On left a seedling with roughened leaves resulting from similar treatment four weeks previously.

effect. A series with 50 seeds each treated with 0.4 per cent solutions for 1, 2, and 4 days has given plants with 56, 94, and 100 per cent ± 4*n* tissue, as determined by appearance. Only part have flowered as yet, but the pollen records so far obtained confirm the judgments from appearance as to the relative effects of the different lengths of treatment upon production of 4*n* branches. Records now being taken suggest that increased temperatures during treatment may increase the proportion of 4*n* branches.

All the above experiments were made with our standard Line 1 Jimson Weed (*Datura stramonium*). As controls, 243 plants of this line from untreated seeds were grown this past summer. They were all shown by the pollen test to be normal *2n*.

Seed Treatment of Other Species

It has been already mentioned that swollen stems of *Datura* seedlings are an early indication of chromosome doubling. In certain other species the swelling is more conspicuous than in *Datura*. Figure 4*B* shows a pot of *Cosmos* seedlings, grown from seeds which had been treated with 0.05 per cent colchicine for 4 days. They were photographed about two weeks later. Their conspicuous swollen stems are in contrast to those of the control (Fig. 4*A*). Figure 4*A'*, *B'* shows typical *Cosmos* seedlings from the control and treated pots of Figure 4*A*, *B*. Swelling of seedling stems and inhibition of root growth are characteristic of seedlings from treated seeds. Often the seedlings from heavy treatments are washed away when the seed pans are watered on account of having insufficient roots to anchor them in the soil. Various procedures have been tested with more or less success to ensure a treatment of the growing point of the shoot without checking the growth of roots. These include starting germination and production of roots on plain agar before covering the seeds with solutions of colchicine in water or dilute agar, and attempting in various other ways to confine the application to the plumule. It might be possible by the use of growth-promoting substances to induce the production of normal roots on stunted seedlings.

Portulaca grandiflora is one of the most convenient species with which to carry on bioassays of colchicine. It can be made to germinate in two or three days in a half cc or less of fluid in small vials and the results can be read off after four to five days.

Figure 6*B* shows a series of seedlings of *Portulaca* six days after starting treatment. Reading from right to left they represent plants grown in 0.0125 per cent, 0.00625 per cent, and successive solutions of half the previous concentration down to 0.0004 per cent. The plant at extreme left is a control grown in tap water. The photograph is a poor representation, but shows the progressive checking of root growth with increasing concentrations. The swellings below the cotyledons are more distinct in the living condition and are evident in the 0.0004 per cent solution. A *Portulaca* unit for the bioassay of colchicine might be established as that concentration at which half of the hypocotyls show characteristic swelling.

By tests with *Portulaca* we have determined that colchicine can be sterilized in solutions in the autoclave without deterioration and that it remains unaffected by light or by standing, at least for considerable time. Its relative stability is a convenience in treatments. The same solution may be used repeatedly.

By the use of seeds of Portulaca and different derivatives of colchicine, a series of experiments has been started in cooperation with Dr. Roger Adams of the University of Illinois to determine if possible what specific groupings of the colchicine molecule are necessary for the action of this chemical in doubling chromosome number.

Methods Other Than Seed Treatment

Immersion method. While our first tests were with seeds, successful methods for treating other parts of the plant have been developed. One of the simplest is immersion of a twig in the solution. With flexible stems such as those

of *Portulaca* shown in Figure 5*A* this method is easily applied. The effect is greater if the stems or leaves are cut before immersion. By this method we have induced 4*n* tissue in *Portulaca* by the use of 0.025 per cent solutions for one day, as well as by use of stronger solutions.

Solutions in agar. For rigid upright stems solutions in 0.8 per cent agar have been found more convenient than fluid solutions. Figure 5*B* shows plant with tip covered with a vial of agar solution. A relatively wide mouthed vial is more convenient than a narrow one which would limit the amount of growing tissue included. Figure 2*D* shows two plants which had been treated with a solution of 0.1 per cent colchicine in agar for two and three days respectively, 19 days before the photograph was taken. The portion which had been enclosed in the agar solution has grown out with rough leaves, while the untreated lower leaves are normal in appearance. The plant on the left produced a flower with 80 per cent of the pollen of the size from 4*n* tissue, while a flower of the plant on the right had 95 per cent of such large grains suggesting origin of a part of this flower from tetraploid tissue.

Another method with agar solutions is to apply them while warm and fluid in drops so as to cover the buds to be treated. In a few days the agar dries down to a skin which is sloughed off by the growth of the plant. Apparently the concentration of colchicine in agar needs to be higher to give effects comparable with fluid solutions.

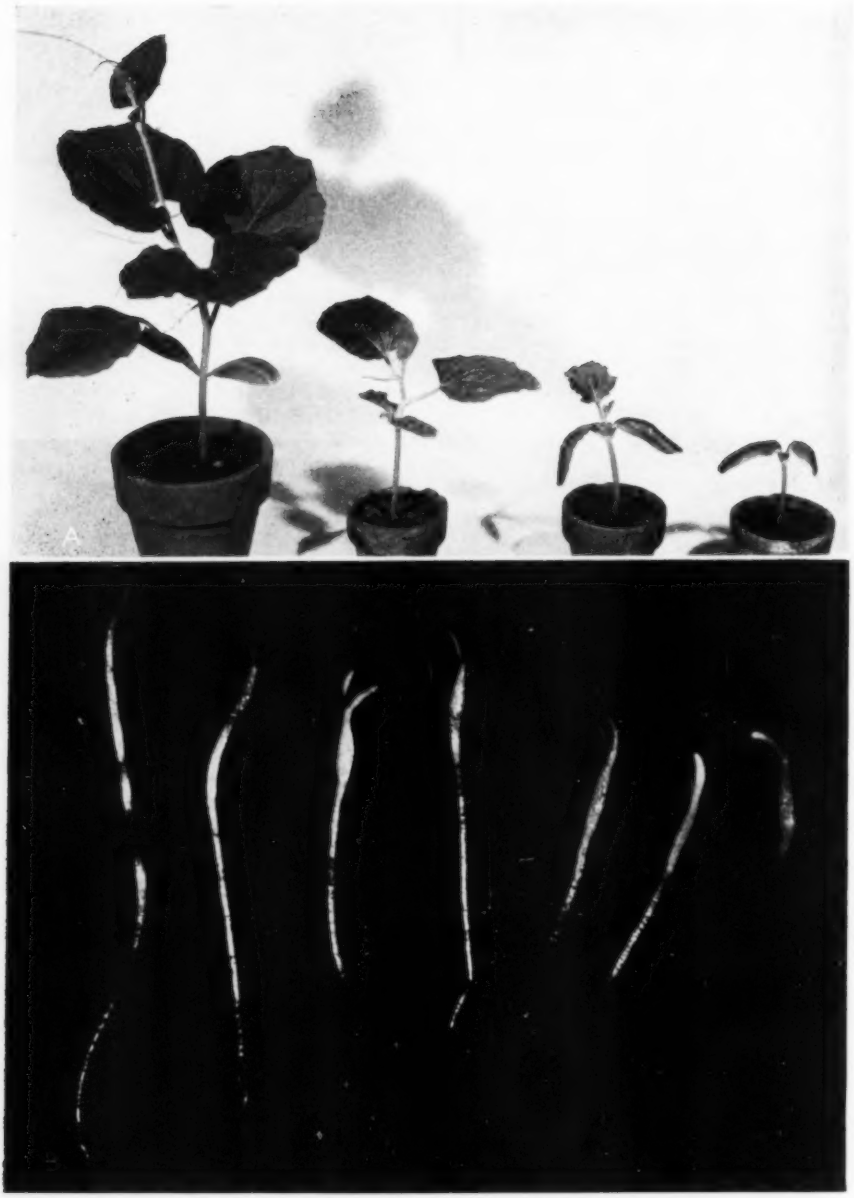
Mixtures with lanolin. Mixtures with lanolin have been successfully used in inducing 4*n* tissue. Concentrations are needed considerably higher than with solutions. The lanolin is less easily weighed out and the amount used difficult to control. It is a messy method which we have largely discarded for herbaceous plants, but it might be of value for special purposes.

Capillary string. The essential requirement of methods of treating parts of adult plants is to bring the solutions into contact with the buds without injuring the other parts necessary for photosynthesis, the activity of which may force out the mutated tissue. A capillary string with one end immersed in solution and the other end wrapped around the buds has been found to be an effective way in which to bring the active agent in contact with the meristematic tissue. This method is shown in Figure 5*C*.

Single drop. A method economical of amount of fluid used is the application of a single drop of fluid to a bud, with several successive repetitions of the application during one or more days as the drop is absorbed or dries up. Figure 5*E* shows a drop from a capillary glass pipette being applied to a young seedling of *Datura*. The plant on the left with roughened leaves had been similarly treated four weeks previously. Figure 6*A* shows an untreated squash plant on left as control and three plants which had been treated in the cotyledon seedling stage with respectively 4, 12, and 30 drops of 0.4 per cent colchicine. The more drops applied the more the plants have been checked. With 30 drops the growth of the plumule has been entirely inhibited, while with 4 and 12 drops a decrease in growth is evident with roughness of leaves.

Figure 7 shows two tobacco plants from the cross *Nicotiana tabacum* × *N. glutinosa* which are about a month old from planting. The one on the left is an untreated control and on account of its parentage must be a sterile hybird. The one on the right is a sib seedling from the same capsule but has been treated with 4 drops of 0.4 per cent colchicine. Its roughened leaves indicate 4*n* tissue. If this involves a flower a double diploid pure-breeding race will have been established.

Atomizing. Another method of getting a limited quantity of solution on growing points is by means of a fine spray from an atomizer. Figure 5*D* shows an arrangement which has been found convenient. The spray tank furnishes air pressure. The compressed air cut off valve, which is being depressed with thumb of left hand, controls the spray. It was bought from a dental sup-



COLCHICINE TREATMENT INHIBITS GROWTH

Figure 6

A—Four squash plants;—untreated control on left; on right, plants which had been treated successively with 4, 12 and 30 drops of 0.4 per cent solution of colchicine. The slowing of growth is proportional to strength of dosage. The highest dosage has entirely inhibited growth

ply house. The atomizer held in the right hand was purchased in Woolworths for twenty cents and on account of its small size is adapted to the small quantities of solutions used. Figure 2*C* shows a 3*n* plant which had been sprayed 34 successive times with a 0.4 per cent solution. It was photographed 24 days after beginning of treatment. The older leaf on the left that was untouched by the treatment is normal in appearance. Partially grown leaves were wetted by the solution only on the upper side and consequently the differential growth has caused them to buckle downward. The smaller leaves toward the center are strongly roughened. If the colchicine becomes effective in doubling the chromosomes of this triploid plant we should have a 6*n* or hexaploid individual which may be used in various crosses, as will be indicated later.

A method of treatment which we thought might be of value turned out unsuccessfully. Bottle grafts were made with a long projecting leg which was kept in a bottle of water until good union was established between scion and stock. The legs of the scions were then inserted into bottles containing respectively 0.1, 0.025, and 0.00625 per cent colchicine and the experiment was continued for 1, 2, and 4 days. During this period the plants were kept sparingly watered, nearly to the point of wilting. The leaves on the more heavily treated scions were killed by the alkaloid, but practically no roughened leaves were induced and no flowers with large pollen grains were developed on later growth. A preliminary experiment in which cuttings of *Portulaca* were treated by immersing their cut ends in solutions of colchicine and later rooting the cuttings in sand have so far given negative or inconclusive results.

Through the use of colchicine with the methods of treatment outlined above we have succeeded in inducing changes which are interpreted as due to doubling of chromosomes in the following genera: *Datura* (several species), *Portulaca* (2 species), *Cosmos* (2 species), *Phlox, Stellaria, Petunia, Nicotiana, Digitalis, Mirabilis, Tropaeolum, Cheiranthus, Raphanus, Cucurbita, Trifolium, Medicago, Zea, Allium.* So far no limit has been found to the species which can be successfully treated with colchicine. Judging from experiments with mosses there probably is a limit to the number of times the chromosomes of a given species can be doubled.

In *Datura* and *Portulaca* we have secured flowers with 8*n* as well as 4*n* tissue by treatment of 2*n* seeds. By treating 4*n* seeds of *Datura* we have secured a flower all of the pollen of which was of the size expected of an octoploid (8*n*).

In *Cosmos* and the common chickweed (*Stellaria media*) we have induced flowers with 4*n* tissue by spraying with colchicine. The chickweed was sprayed unintentionally while treating *Datura* plants in pots in which young seedlings of chickweed were growing as weeds. Some which developed rough and swollen leaves we believed had been affected by the treatment. They were therefore saved and induced to grow into flowering condition, when pollen examination showed that some had developed 4*n* branches.

Chromosome Determination by Pollen Size

In balanced chromosomal types a short-cut method of determining the number of chromosomes is afforded by the size of pollen grains. The method has been extensively checked during many years experience and has been found reliable. The volume is proportional to the number of chromosomes

LEGEND TO FIGURE 6—CONTINUED

of the plumule, while the lesser treatments have roughened the leaves as well as decreased the stature of the plants. *B*—Seedlings of *Portulaca* six days old. That on the left is the control, grown in tap water. The one next to it was grown in 0.0004 per cent colchicine and each one to the right was grown in a solution twice as concentrated. The last was grown in a 0.0125 per cent solution. Note the checking of root growth with increasing concentrations and the swelling of the stem below cotyledons of treated seedlings.

which the grain contains, provided the chromosomes are in the balanced condition. Volumes are not closely related to the number of unbalanced extra chromosomes which may be present, but our immediate problem has to do with doubling the whole chromosome complement. Pollen grains of a tetraploid have $2n$ chromosomes and their volume is twice that of the $1n$ grains of a normal diploid ($2n$) plant. The diameter of the former grains is 1¼ times that of diploids. Throughout this paper we have spoken of $2n$ and $4n$ tissue. It should be remembered that in the pollen grains the chromosome number is reduced to half so that $2n$ tissue will have $1n$ pollen and $4n$ tissue will have $2n$ pollen grains.

We are aware of no exception to the rule that within a given form the size of pollen grains is proportional to the number of chromosomes which they contain. Doubling of chromosomes, however, may occur under exceptional conditions during the reduction divisions and thus lead to giant grains with doubled chromosome number in the anthers of $2n$ flowers. This may be induced by the environmental factors cold[10] and heat.[14] Doubling of chromosomes during reduction may also be brought about by genes which affect chromosome behavior. Of such genes there are several known in *Datura*.[15]

Among other cells that have been used to determine chromosome number by differences in size are the guard cells of the stomata which appear to be less influenced by environmental factors than many other cells of the plant.

Figure 8 shows photographs of pollen of normal diploid ($2n$) *Datura stramonium*, compared with pollen obtained from an induced tetraploid ($4n$) and from an induced octoploid ($8n$). Dr. Bergner has confirmed the pollen determinations of the induced $4n$ and $8n$ tissue by counts of the chromosomes.

Examination of pollen has shown that polyploidy has been induced in *Portulaca grandiflora*. Pollen from $4n$, $8n$, and mixed $2n$ and $4n$ tissue has been obtained. Pollen determinations of induced $4n$ tissue in *Portulaca* have been confirmed cytologically by Dr. H. E. Warmke. Flowers with mixed $2n$ and $4n$ tissue might be expected to form seeds which would give rise to a mixture of $2n$, $3n$ and $4n$ offspring.

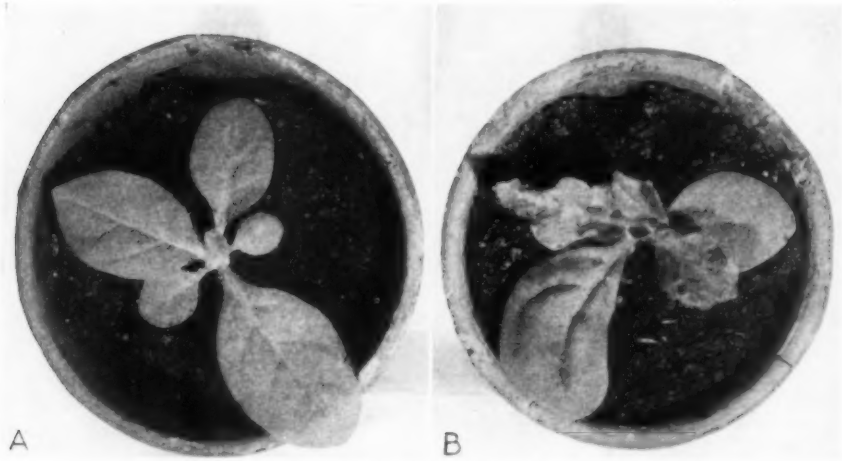
Figure 9 shows photographs of pollen of squash, that of a normal diploid ($2n$), as compared with pollen from a flower on induced tetraploid ($4n$) tissue.

The pollen determinations in the present study have been made chiefly by J. L. Cartledge and E. A. Weaver.

Advice to Experimenters

Some appear to expect too much from doubling chromosomes by use of colchicine. One correspondent asks "If it will grow better plants, is it good for hair on the head?" and similar questions have been asked by others. Not all the effects of chromosome doubling are advantageous economically. Thus, tetraploid maize and citrus fruits are of inferior quality, although our best varieties of apples are polyploids. Moreover increase of chromosome number may retard development and thus lead to plants with smaller rather than larger stature. Juggling chromosomes for the betterment of plant-kind is primarily a matter for the trained genetics engineer who knows the chromosomes with which he is working. In one field, however, that of floriculture, the chances of success appear promising and the technique necessary is relatively simple for those familiar with the use of a microscope.

Numerous inquiries have been made regarding source of supply of colchicine and the question has been asked whether the drug can be used by the amateur gardener in manufacturing races of plants with larger blooms. We have used the colchicine alkaloid amorphous, which is obtainable from all the larger drug firms. Its price varies somewhat with the firm and with the quantity ordered. The cost ranges around $25.00 per ounce, but quantities as small as ⅛ ounce may be purchased. This would be sufficient for a considerable series of experiments if used as concentrated as 0.4 per cent, which is too strong for some species. Drug firms have warned us that colchicine is highly poisonous and



SPECIES HYBRID SHOWS CHARACTERISTIC EFFECTS

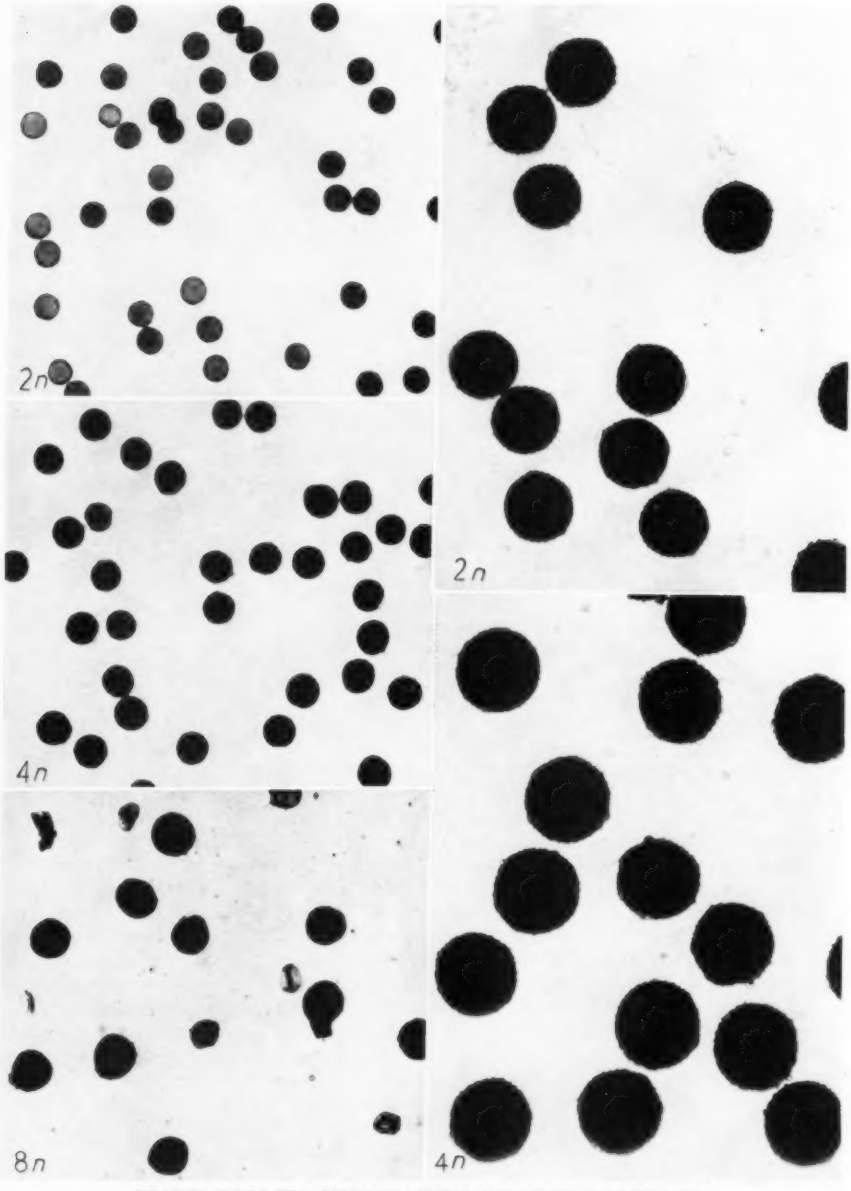
Figure 7

Seedlings from the cross *Nicotiana tabacum* × *N. glutinosa*. This cross ordinarily produces a completely sterile hybrid. The seedling at *A* is an untreated control plant and will undoubtedly be unable to produce seed on account of its sterility. The seedling at *B* has been treated with four successive drops of a 0.4 per cent colchicine solution and from its roughened leaves appears to have 4*n* tissue. If 4*n* flowers are formed, as seems likely, the sterile species hybrid will have been transformed into a pure-breeding double diploid with doubled number of chromosomes.

should not be allowed to be absorbed by the skin.

If one imagines that one can spray a plant and it will at once produce more vigorous growth and bigger blossoms, there is sure to be disappointment. The plant is checked in growth by the poison and in slowly recovering produces crumpled, roughened leaves and confused branching,—the type of plant one would naturally discard as undesirable. Some of the branches that recover enough to produce flowers will have the normal 2*n* constitution of the race started with, while other recovered branches will have 4*n* tissue, seeds from which will give the desired 4*n* race in the next generation. It is only in the generation following the treatment, therefore, that the large flowered races free from admixture with 2*n* tissue would be expected. The problem is to detect on the mixed tissue of the treated plant, the 4*n* flowers from which to save seed. One might guess at the determination from appearance of leaves and flowers, but this would be uncertain and almost surely lead to useless effort. We cannot advise the amateur to attempt to obtain polyploids without the use of a microscope with which to identify the flowers with doubled chromosome number by their enlarged pollen grains. The procedure, however, is rather simple. We examine the pollen in a solution of 45 per cent acetic acid rendered an amber color by the addition of a small amount of iodine. An eyepiece micrometer may be of use in measuring the pollen grains to be compared, especially if one is working with several different species which have pollen grains of different sizes. Any high school biology teacher should be in position to help one in getting familiar with the relatively simple methods which are involved in the use of a microscope for examination of pollen.

When handling a single species one soon becomes familiar with the normal grains of 2*n* flowers and the grains of 4*n*



GIANT POLLEN SHOWS CHROMOSOME DOUBLING

Figure 8

Pollen of normal diploid (2*n*) *Datura stramonium* and from a colchicine induced tetraploid (4*n*); and octoploid (8*n*). The size of pollen grains is approximately proportional to the number of complete sets of chromosomes they contain.

Figure 9

Pollen of squash, from a normal diploid (2*n*); and from a tetraploid flower (4*n*) induced by colchicine treatment. In using colchicine the size of the pollen offers a quick and fairly accurate way to locate polyploid plants or sectors.

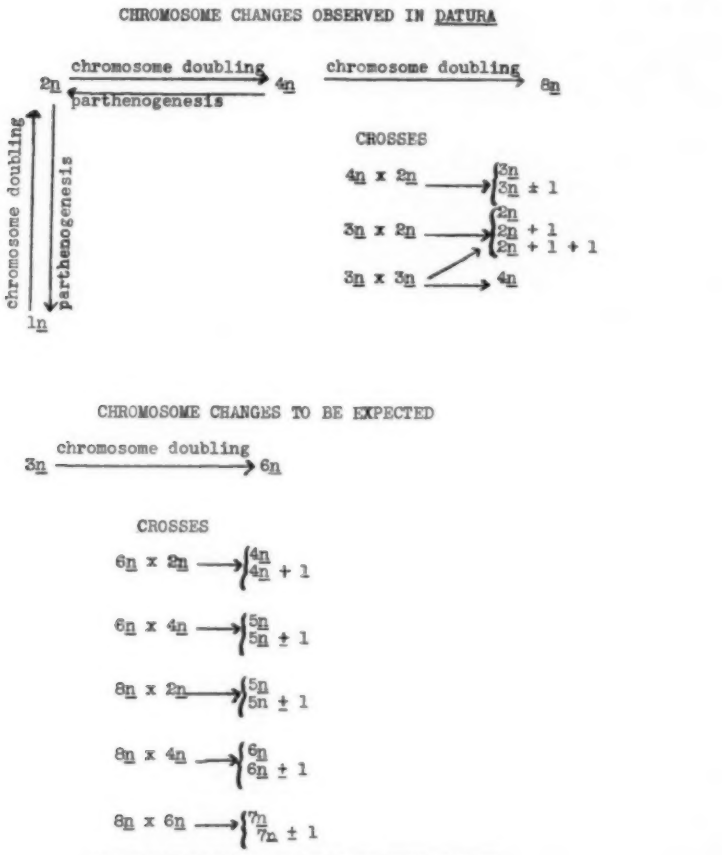
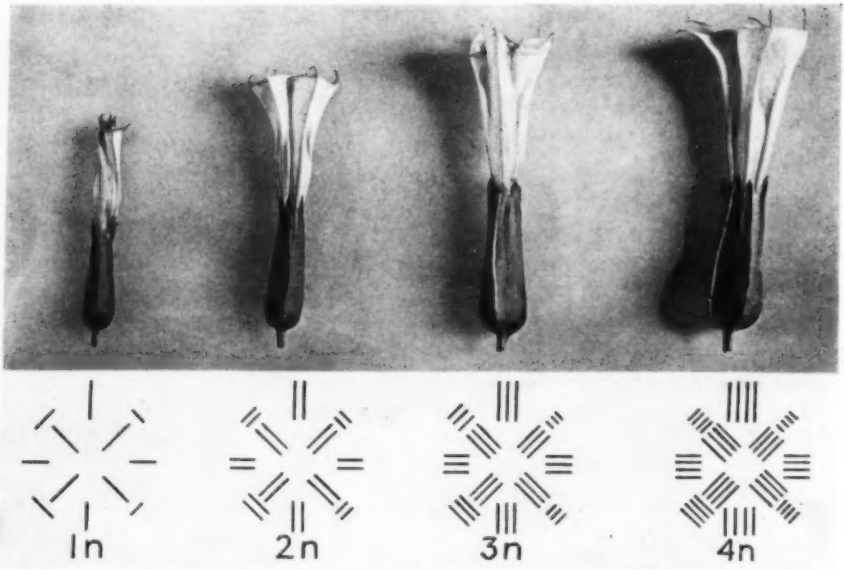


Figure 10

Diagram to show chromosomal changes observed in *Datura* and those which may be expected. The formation of haploids and tetraploids from diploids has been observed a number of times in more than 20 years' study of the species. Triploids have been produced by crossing $2n$ and $4n$ races, but the production of hexaploids from a doubled triploid has not yet been accomplished. Colchicine treatment only speeds up a process which occurs naturally at rare intervals, and offers the possibility of quickly getting results which might take a lifetime if one waited for the more leisurely process of nature.

flowers appear large and conspicuous. To determine the chromosome number by making a microscopic preparation and actually counting them is a tedious procedure requiring special technique even if the relatively simple iron-aceto carmine method is followed. It is an unnecessary luxury for the present purpose. The pollen method has an added advantage in that the flower may first be selfed and the remaining pollen used for the determination, whereas by taking a young bud for chromosome counts one may be putting out of commission the only bud formed by a strongly affected plant and then find it was not at the proper stage for chromosome counting. Different species will require different strengths of solutions and different methods of treatment. It would seem



INCREASE IN FLOWER SIZE WITH INCREASE IN CHROMOSOME NUMBER

Figure 11

In some species, an increase in the number of complete chromosome sets is accompanied by an increased plant size, as in the Datura series shown above, where there is a consistent increase in size of flowers from the haploid (1*n*) through the tetraploid (4*n*) forms. It is not to be expected that the results obtained by chromosome doubling will be equally consistent with all species or always lead to varieties of economic value.

advisable, therefore, for the amateur to confine his efforts to a single species.

We have spoken of methods which we have used in treating plants reproduced by seed. Plants propagated vegetatively present somewhat different problems. As shown by Figure 3*C*, a typically clean-leaved 4*n* branch may grow out from the roughened mixed tissue. If such 4*n* branches are propagated vegetatively, they should give rise to 4*n* clones. Such clones would have an advantage over seed reproduction for highly hybridized types like the cultivated varieties of iris for example, since they retain the characteristics of the plant which was treated except for changes such as increase in size of flowers which are associated with tetraploidy. Seed reproduction of highly hybridized forms leads to a variable progeny and the parent type may fail to appear in the offspring. Treatment of seeds of such forms for the reproduction of tetraploids, therefore, would be of limited floricultural value.

It must not be forgotten that in all breeding work there is an element of gamble. Not all polyploids may be desirable. Doubling chromosomes may unduly retard development and thus reduce the abundance of flowering, although the individual flowers may be enlarged. The limits of making new races with larger flowers by doubling their chromosomes have not yet been explored. This is a fertile field in which many laborers are needed. It is a field which is open to the intelligent amateur who can acquire a microscope and learn to look at pollen.

Value of Chromosome Doubling

If control of chromosome doubling by chemical means proves to be of general application, as seems to be the case, a tool of considerable value for chromosomal analysis will be available to the

geneticist interested in theoretical problems. By its use, moreover, the practical plant breeder will be able to work with greater precision in his efforts to control the evolution of economic forms both of plants propagated vegetatively and of those reproduced by seed. The adjoining diagrams (Figure 10) show the chromosomal changes which have been obtained in *Datura* and also the added changes which we should be able to obtain now that a ready method of doubling chromosome number seems available. The balanced polyploid types, $3n$, $4n$, $5n$, $6n$, $7n$, and $8n$, which have an equal number of chromosomes of each kind, form the basis of a considerable number of unbalanced types with individual extra chromosomes. The $2n + 1$ types in *Datura*, for example, have been used in analyzing the genic constitution of the different chromosomes within this genus, in locating genes in individual chromosomes, and in building up pure-breeding types with extra chromosomal material. The primary $2n + 1$ types of any species that is being intensively studied may be obtained by means of an induced tetraploid. The cross $4n \times 2n$ produces triploids ($3n$). The offspring of triploids contain simple ($2n + 1$) and double ($2n + 1 + 1$) trisomic forms which may be used for genetic analysis or which may be of economic value. New types with extra chromosome material have been discussed in a recent number of this JOURNAL[2] and some of the possible practical applications of polyploid forms have been pointed out by the senior author in a 1937 Year Book separate of the Department of Agriculture.[5] Both $3n + 1$ and $3n - 1$ types, as well as triploids, have been obtained from the cross $4n \times 2n$ since there is a high percentage of non-disjunction in $4n$ plants.[1] A high percentage of non-disjunction would also be expected in polyploids of a higher order and, hence, an extensive series of $+ 1$ and $- 1$ and more complicated types should be obtainable with different degrees of unbalance if and when the types suggested in the diagram are secured. It might be pointed out that triploids have an additional value in forms that are propagated vegetatively since they are sterile or produce only a few seeds from selfing and, in consequence, may allow a plant to flower continuously without being checked by seed setting.

Some of the plants from treated seeds were suspected of carrying deficiencies on account of their abnormal appearance. This suspicion has been confirmed cytologically by Dr. Bergner and will be reported upon later. There is some evidence that treatment with colchicine increases the proportion of pollen lethal mutations. It would appear therefore that the genetic effects of colchicine are not confined merely to doubling chromosome number.

Possibly one of the most important uses of chemical methods of inducing chromosome doubling will be in making double diploids out of sterile species hybrids. Such forms will assist in the analysis of differences between species. It may be mentioned in this connection that such doubling of chromosomes is about the only well established mechanism known among plants for the evolution of species. Double diploids from sterile hybrids will be of economic importance since they should establish pure-breeding races with hybrid vigor and the desirable characteristics brought about by tetraploidy. Judging from the appearance of the treated seedlings (Figure 7) we have succeeded in obtaining an abundance of double diploids from sterile hybrids between *Nicotiana tabacum* and *N. glutinosa* from seed kindly sent us from Dr. F. O. Holmes. Malformed seedlings of this hybrid with thick rough leaves have also been secured by treating the seeds before planting. The occurrence of double diploids from this cross has been reported, but they have been extremely rare.

In at least two respects plants appear more favorable than animals as subjects in which to double chromosome number. Plants have growing points which may reproduce the whole organism. Hence a part of the plant in which doubling has occurred may usually be induced to grow out into a $4n$ branch and bear

seeds or the branch may be propagated vegetatively. Most plants have the sexes on the same rather than on separate individuals as is the condition in the higher animals. In consequence, doubling chromosomes in a single branch of a Jimson Weed, for example, should lead to a 4*n* race of *Daturas,* but doubling chromosomes in a limb of a lobster would not effect the next generation. In animal forms in which the fertilized egg can be subjected to treatment at an early stage and then carried to full development, it may be possible to secure tetraploid individuals.

The senior author has experiments under way in cooperation with Dr. G. C. Embody and A. M. Phillips of the Cornell Laboratory of Fish Culture and S. C. Walters, Superintendent of the Cold Spring Harbor State Fish Hatchery, in which attempts are being made to induce tetraploidy in trout by treatment of eggs. So long as the eggs of such higher vertebrates as mammals cannot be subjected to treatment and then brought to develop into adults they will form poor subjects for polyploidy experiments. It is theoretically possible that local tetraploidy might be induced in the ovaries and testes with the subsequent production of eggs and sperm with doubled chromosome number. Our experience with plants, however, would lead us to expect greater likelihood of success in animals from attempts to induce doubling in the fertilized egg.

Müntzing[13] in a recent paper has discussed the characteristics and role in evolution of tetraploids and other polyploids. It will not be necessary to extend the discussion in the present paper. Tetraploidy and presence of unbalanced extra chromosomes are known to have been factors in the origin of a large proportion of our most desirable varieties of fruits and flowers. In addition to increase in size of organs of the plant, such as the flower (Figure 11), there is evidence that doubling chromosome number may change a sterile to a fertile form, a dioecious to an hermaphroditic race, an annual to a perennial, and may increase winter hardiness. The ability to induce chromosome doubling, therefore, is of importance to practical as well as to theoretical genetics. With increasing knowledge of the constitution of chromosomes and of methods whereby their structure and behavior may be altered, there arises an opportunity for the genetics engineer who will apply knowledge of chromosomes to building up to specifications forms of plants adapted to the surroundings in which they are to grow and suited to specific economic needs.

Table I. Effects of immersing seeds of Datura stramonium for ten days in different concentrations of colchicine.

Pedigree number	% colchicine	Determination by appearance		Determination by pollen size.							
		Total	% ± 4n	2n	4n	2n + 4n	4n + 8n	2n + 4n + 8n	Total	±4n	% ±4n
3602013	0.003125	24	0	24	-	-	-	-	24	0	-
3602012	0.00625	25	0	24	-	-	-	-	24	0	-
3602011	0.0125	23	0	23	-	-	-	-	23	0	-
3602010	0.025	25	0	25	-	-	-	-	25	0	-
3602009	0.05	23	0	22	-	-	-	-	22	0	-
3602008	0.1	23	8.7	23	-	-	-	-	23	0	-
3602007	0.2	24	87.5	10	3	4	2	1	20	10	50.00
3602032	0.2	24	75.0	12	8	3	1	-	24	12	50.00
3602031	0.4	23	65.2	12	6	3	1	-	22	10	45.45
3602030	0.8	18	83.3	7	8	2	-	1	18	11	61.61
3602029	1.6	18	66.7	6	4	3	2	2	17	11	64.71

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COLCHICINE AND DOUBLE DIPLOIDS

MANY readers of the JOURNAL will be interested, we feel sure, in some expansion and explanation of certain points not touched on in Dr. Blakeslee's article, which have come up in connection with this most interesting subject.

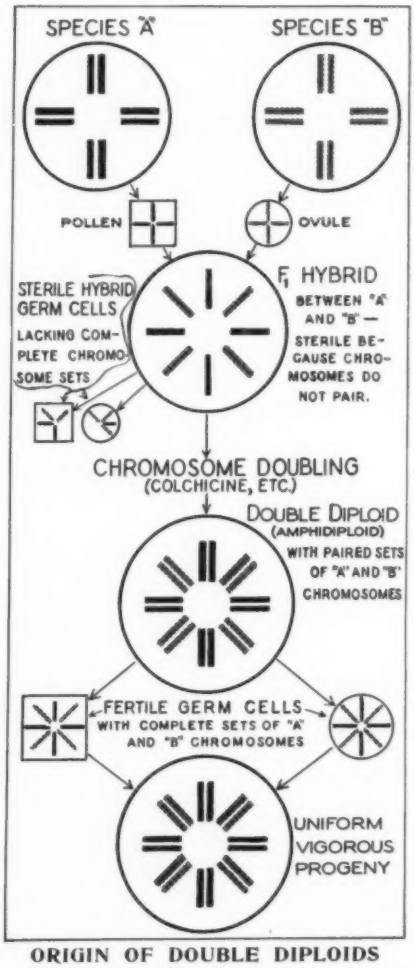
The tidal wave of wierdly misleading publicity distributed by the Hearst newspapers on November 21, has doubtless aroused hopes and fears that have no foundation whatever. Colchicine is not a "growth elixer," and evidence is lacking as to its effects on animal chromosomes, so that doctors may still make their calls safe from attack by giant rats, and ladies are in no danger of being gobbled up by caterpillars suddenly gone carnivorous.

Colchicine is a narcotic alkaloid, related chemically to morphine and codeine. It is a very potent and very poisonous substance whose immediate effect on growing tissues even in very small concentrations is to produce stunting and distortion. It offers no Magical Royal Road to the production of new varieties of plants and animals. In spite of the cold water which must be thrown on over-enthusiastic popularizations, the effect which colchicine has on doubling the number of chromosomes in the cells makes it unquestionably one of the most important genetic discoveries of the year.

One of the most hopeful fields of practical application would seem to lie in the possibility of producing experimentally vigorous fertile forms from sterile species hybrids. Heretofore the plant breeder has had his activities in this direction seriously limited because a cross between two forms differing materially in chromosome constitution, even though the hybrid plants were capable of developing and flowering, produced neither fruit nor seed. For that reason, species hybridization has been a blind alley as far as the plant breeder is concerned, with notable exceptions of course, where asexual reproduction makes possible utilization of such sterile hybrids. By treatment with colchicine, sterile hybrids may all at once have an entirely new interest to the plant breeder. In several instances spontaneous doubling of the chromosomes in such forms has been observed,—resulting in the production of fertile, true breeding forms, with a chromosome number equalling the sum total of the somatic chromosome numbers of both parent species. The mechanism involved in this chromosome doubling with the consequent fertility (amphydiploidy) is explained in the accompanying drawing. Such double-diploids are interfertile and produce vigorous and uniform progeny because, arising as they do from a doubling of unpaired chromosomes, they represent essentially pure lines, and not only pure lines, but pure lines very likely to exhibit hybrid vigor! The practical implications of this to the plant breeder are obviously of very great promise. As yet, of course, the possibilities have not been explored at all and unforeseen difficulties may bring disappointment. Enough observations on spontaneous chromosome doubling have been made to leave little doubt that in many situations this method may prove extremely valuable.

There are many special situations in which the production of amphydiploids may be of great practical importance, one of the most promising of these being in connection with tree genetics. It has become painfully clear that an adequate supply of lumber to meet the increasing demands of modern industrial civilization has put a disastrously heavy drain on natural supplies of timber. The need cannot fully be met by reforestation and conservation projects, unless conducted on a huge scale. Superior trees, produced by breeding, would be a great help. Several attempts* have been made to apply genetic methods to meet the emergency, but the difficulties are many and formidable. Trees are notoriously slow to mature with a discouragingly long interval between one generation and the next. To produce the pure lines necessary for genetic experimentation would require centuries. Some progress has been made in the development of hybrid forms which can be propagated from cuttings, and these offer real promise in certain special cases. It has become increasingly clear that such techniques hardly offer a general solution of the problem, and that tree genetics in general is a disappointingly long-term and not overly hopeful approach to the timber problem. Recently Anderson† has suggested that by interplanting male and female trees of two dioecious species, hybrid seed might be produced in great enough abundance to plant large areas. The difficulty with this admirable plan is that very few timber trees are conveniently arranged like the ashes in two sexes, so that the method is applicable. The conifers and most of the hardwoods either have perfect flowers, or both male and female flowers on the same tree. The production of amphydiploids from sterile hybrids between two different species offers a method which may have much wider application because it may be useful wherever hybrids can be obtained.

On the theoretical side, alluring possibilities also present themselves. A few months ago a description was published in the JOURNAL‡ of a trigeneric hybrid between maize and its two closest relatives, containing a complete chromosome set of each of the three parent genera. Should colchicine treatment succeed in producing a three-cornered amphyidiploid from this hybrid, this might well be fertile. The long search for experimental or archaelogical light on the origin of maize may be entering a new phase as the result of this discovery. Incidentally some of the forms which might arise may prove to have great practical value.—ED.


SPECIES "A"
SPECIES "B"
POLLEN
OVULE
STERILE HYBRID GERM CELLS LACKING COMPLETE CHROMOSOME SETS
F1 HYBRID BETWEEN "A" AND "B" — STERILE BECAUSE CHROMOSOMES DO NOT PAIR.
CHROMOSOME DOUBLING (COLCHICINE, ETC.)
DOUBLE DIPLOID (AMPHIDIPLOID) WITH PAIRED SETS OF "A" AND "B" CHROMOSOMES
FERTILE GERM CELLS WITH COMPLETE SETS OF "A" AND "B" CHROMOSOMES
UNIFORM VIGOROUS PROGENY

ORIGIN OF DOUBLE DIPLOIDS
Figure 12

This chart shows in rough outline, the main features of making a fertile hybrid from a sterile hybrid by chromosome doubling. Compare with cover illustration, which shows an autotetraploid with chromosomes in groups of four.

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*AUSTIN, LLOYD, Breeding Pines for More Rapid Growth, *Journal of Heredity*, July, 1926. SCHREINER and STOUT, Results of a Project in Hybridizing Poplars, *Journal of Heredity*, June, 1933.

†ANDERSON, EDGAR, and C. M. WELDON, Studies in the Genus Frazinus, *Journal of Heredity*, December, 1936.

‡MANGELSDORF, P. C., and R. G. REEVES, A Trigeneric Hybrid of Zea, Tripsacum, and Euchlaena, *Journal of Heredity*, December, 1935.

INHERITANCE OF A WHITE FORELOCK

Through Five Successive Generations in the Logsdon Family

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THE first record of a white forelock was published by Rizzoli in 1872 when he reported on forty-nine individuals in six generations. Several other reports dealing with this subject have been published since the paper of Rizzoli but with only a few photographs. Among these later reports was one by Miller in 1915 concerning the Little family which was traced back to a child by Sir Percy Little of England who died in 1403.

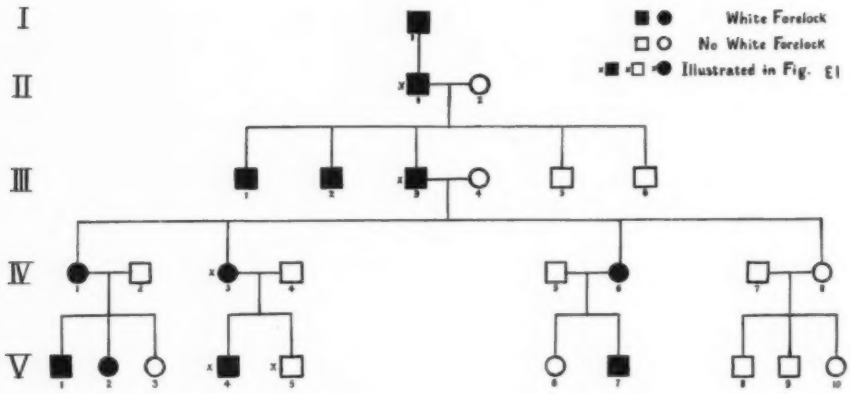
The case of the Logsdon family now being reported is unique in that there are available photographs of many of the individuals of four generations. As far as it has been possible to ascertain, photographs of only two generations in other families exhibiting the white forelock have been published. The white forelock in the Logsdon family first appeared in about the middle of the eighteenth century, and has been transmitted through five successive generations to the present time.

The earliest photograph is of a son in the second generation, Figure 13-II. This man produced a son with the white forelock, Figure 13-III. The son had four daughters, three of whom exhibited the white forelock. The other daughter, Figure 14-IV-8, produced three children also without white fore-

FOUR SUCCESSIVE GENERATIONS INHERIT DOMINANT WHITE FORELOCK

Figure 13

II, the great grandfather. III, the grandfather. IV, the mother. V, the two sons, one inheriting the white forelock and the other not inheriting it.



FIVE SUCCESSIVE GENERATIONS SHOWING DOMINANT INHERITANCE OF A WHITE FORELOCK IN THE LOGSDON FAMILY

Figure 14

I-1, the first recorded ancestor having a white forelock. II-1, his son inherited the white forelock and married a woman without it. III, of their five sons three inherited the white forelock and two did not. IV, showing the four daughters of one son, III-3, three daughters having inherited the white forelock and one has not. V, showing the children of these four daughters who married men without a white forelock; some of the children of each of the three mothers possessing the white forelock have inherited it but none of the children of the other mother not possessing it have the white forelock.

locks, which seems to indicate that unless this characteristic is possessed by a parent it does not appear in the following generation.

The daughter pictured in Figure 13-IV had two sons; one exhibits the white forelock and the other does not show it.

The white forelock is often accompanied with a few white spots in the skin on various parts of the body. This may indicate that the white forelock is a phase of a spotting condition which is conspicuous only when appearing in the hair on the head. Skin spotting occurred in the individuals, Figure 14, IV-6, V-2 and 12. The individual, V-5, has a white spot on one leg but none in his hair. He is the only member of the family known to be so marked.

The author wishes to acknowledge his indebtedness to Donald F. Griess for gathering and assembling the data and to Professor D. D. Whitney for helpful suggestions.

Summary

1. The white forelock seems to be a Mendelian dominant spotting character.

2. It has appeared in five successive generations of the Logsdon family.

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RIZZOLI. *Bullentino delle Scienze mediche Bologna* Sec. V., vol. 23. 1877.

IDENTICAL TWINS IN CATTLE

Their Possible Value in Genetic Research—A Review

WHAT can be learned by studying identical twins in cattle? How can one be sure that a particular pair of twins are in fact identical and not merely fraternal? What facts have already been observed about identical bovine twins? The distinguished leader (since retired) of the animal breeding institute at Berlin seeks to answer these questions in this third article* of a series from that institute. The first article† touched on many of the same subjects, but only 35 pairs of like-sexed twins had then been studied. The second article‡ dealt with the differences between 80 pairs of like-sexed fraternal twins and from it were derived measures of the usual likeness between fraternal twins and of the variation to be expected in that likeness. Against these standards the supposed identity of unusually similar twins could be tested to see whether their similarity was greater than ever would actually occur with fraternal twins.

Besides additional observations on three pairs of identical twins already mentioned in the first article, the present artical describes ten new pairs of identical twins and also three pairs of surprisingly similar twins which, however, were finally decided to be fraternal. Only passing references are made this time to other studies on twins in cattle, as the review of literature in the first article was considered adequate for that. One of the main purposes of the present article is to arouse enthusiastic support for the study of twins in cattle to such an extent that most cases of possibly identical twins would be reported to institutions interested in studying them.

The diagnosis of identity rests on similarity in a long series of characteristics, each of which is determined to a considerable extent by heredity. Fraternal twins might of course happen to be as like each other as identicals in one or a few characteristics but, as the number of characteristics is increased, it becomes more and more improbable that fraternal twins would happen to be alike in all the genes involved, whereas that is to be expected of twins arising from a single fertilized egg.

Method Used Elsewhere

The principle of this method has been used for a long time in such sciences as anthropology where, for example, it may be used to identify an individual as belonging to one or the other of two races which overlap to some extent in every one of their characteristics. If the racial means of those characteristics differ enough, then when many characteristics are taken into consideration, each individual can be definitely classified as belonging to one or the other of the races. For the method to work successfully it is only necessary that there be enough characteristics in which the racial means are different. The greater the difference between those means, the fewer characteristics need be considered to attain the same certainty of identification. The application of this principle to diagnosing monozygosity of twins in cattle encounters some difficulties and brings out many details which will interest those concerned with inheritance in cattle or with identical twins in other species. This application does not seem (to

**Neue Ergebnisse der Zwillingsforschung beim Rind.* C. KRONACHER with the collaboration of D. SANDERS. 205 pictures and 28 curves. 172 pages. 10 Reichsmarks. Also printed as part of Volume 34 of *Zeit f. Züchtt.*, Reihe B: Tierzücht. u. Züchtungsbiologie. Paul Parey, Berlin. 1936.

†*Zeit. f. Züchtt.* 25:1-90. 1932.

‡*Zeit. f. Züchtt.* 32:153-298. 1935.

A TWIN-BEARING FARM

Figure 15

The Dinckenson family, of East Long Meadow, Massachusetts, seems to specialize in twins. The Dinckensons themselves had two pairs, age 15 and 6. Twin lambs and a pair of twin calves complete the picture and furnish twin pets all around. Obviously the human twins are not identical, being of different sex. The calves differ somewhat in marking, so they probably are not identical either. The lambs show a remarkable resemblance, but this may be due merely to a uniformly colored coat. Such an abundance of twins on a single farm might suggest an environmental influence causing multiple births, but considerably larger numbers would have to be accumulated to rule out mere coincidence.

the reviewer) likely to extend general genetic knowledge much. There is, to be sure, the possibility that if enough of these identical twins can be submitted to contrasting environmental treatments, knowledge of the relative importance of heredity and environment and their interactions might be acquired faster than is possible by studying twins in man, where for the most part the experimental method is barred. However, identical twins in cattle are rare and also the relative importance of heredity and environment seems to have (probably *must* have) a different answer for every characteristic in every population; hence it seems dubious that such experiments with cattle, even though they could be made numerous, would contribute much to general genetic knowledge. They might indeed provide some striking demonstrations of the importance of heredity in minute details and in guiding complicated physiological processes.

In the present application of the method to a pair of twins each characteristic is simply graded as "different", "similar", or "surprisingly similar" in the two twins. Numerical values of 1, 2, and 3, respectively, are given to these grades and the numbers are averaged to obtain the "similarity quotient" for that set of twins. For those few characteristics which can be adequately described in centimeters or weights, the difference between the two twins, divided by their average, is expressed as a "percentage difference". The average of these percentage differences for the head measurements (6) is considered as one characteristic in the "similarity quotient". A corresponding average for the body measurements (11) is considered as another characteristic, and the weight difference

is considered as a third. Those average "percentage differences" for the dizygotic like-sexed twins were:

for the six head measurements	4.40 ± .05
for the eleven body measurements	3.53 ± .04
for weight	7.35 ± .47

Other characteristics (22) included in the similarity quotient are:

General conformation
Color pattern
Head markings
Joints
Skin and hair
Horns
Eyes
Teeth
Muzzle pigment
Pattern of muzzle lines
Pigmentation of gums
Constitutional behavior
Physiological peculiarities
Temperament
Psychological peculiarities
Hair whorls
Milk production
Fat production
Blood group
Hemoglobin content of blood
Dry matter in blood
Serum concentration

Naturally there is often room for subjective judgment about whether one of these characteristics in a particular pair of twins is "similar" or "surprisingly similar". The observer must have considerable skill and practical experience to make these ratings standard and reasonably dependable. Even after the similarity quotient is obtained, there is need in some cases for subjective judgment as to whether the twins were in fact identical. The similarity quotients for the 80 pairs of dizygotic twins in the second article ranged from 1.28 to 1.95 and averaged 1.62. For most of the unmistakably monozygotic twins the similarity quotient was about 2.5 to 2.6. But in three sets of very similar twins described here in considerable detail the similarity quotients were 2.05, 2.18, and 2.00, respectively. These three sets were finally adjudged fraternal and are samples of the borderline cases which, in effect, are decided by placing more confidence in some characteristics, such as the pattern of the papillary lines on the muzzle, than in others. However, in most cases the similarity quotient automatically renders the decision.

Determination of Characteristics

The author finds that heredity is of great importance in determining even the minutest details of anatomy and physiological behavior. This is based on the amazing similarity of the identicals. Yet the twins were kept under the same environments, as far as those were controlled, and hence the importance of heredity is not compared with that of environment quantitatively in a way which could be generalized to apply to whole populations. Rather the twins demonstrate *their ability to react alike* to changes in environment. For example, the remarkable closeness with which the daily milk yields of Liese and Lotte rise and fall together (as pictured on page 27) tells little or nothing about the relative importance of heredity and environment in determining milk production but does demonstrate how the twins react almost identically to whatever were the changes in environment which produced the daily and weekly fluctuations in yield. The similarities demonstrate the intricately close control which heredity exercises over the animal's *ability to react* but they demonstrate equally well that the completed characteristic or performance depends much (*how much* they do not say) upon the environment, that is, upon the external stimuli which bring to light the differences in ability to react.

Those identical twins which were observed at intervals during their growing period showed remarkably similar changes in measurements, in temperaments, etc. That is, they were alike at all stages and resembled each other in the details of their growth rates as they did in their mature characteristics. Some growth continues at least up to six years even in skeletal measurements, such as the head measurements, which come close to their mature dimensions at a fairly young age. The author is much impressed with how closely the ante-mortem and the skeletal measurements correspond and concludes that the animal's conformation and general appearance are largely determined by its skeletal foundation.

Most of the identical twins were of

the black-and-white lowland race but some belonged to the red-and-white lowland race, and there was one set of identical twins in the yellow Franconian breed and another in the highland spotted cattle (Höhenfleckvieh).

Similarities in psychic peculiarities are emphasized at many places and "would be recognized by anyone at all familiar with cattle, even though difficult to measure." This will have a familiar ring to many a student of animal breeding who has longed for some simple and fairly adequate mental tests for his animals! Of several sets of twins it is said that "they always kept together while on pasture" and in similar ways seemed to indicate the same preferences and dispositions. On page 108 the breeding and calving records of one pair show that they calved 5 times, never more than 10 days apart, and were bred six times, never more than six days apart. On page 71 are given the dates when a pair of identical twins came in heat for the first fifteen times. This happened first on the very same day and their estrual cycles were so nearly identical that they were only 12 days apart on the fifteenth subsequent heat period, when they were considered old enough to breed.

The wealth of detail in this article may suggest to other workers additional observations or measurements which they might find worth making. (The reviewer, however, has a personal conviction that more experiments are harmed by spending too large a portion of the available effort in taking data and too little in the analysis of those data than by having failed to get pertinent data at the proper time). Examples of the detail here are the post-mortem measurements mentioned on pages 51 to 55, and the analysis of blood and hormone characteristics mentioned on page 72. These are in addition to the routine measurements used in the similarity quotients.

This article is somewhat repetitive and is not easy reading (one sentence on page 157 extends for 28 lines!), but will be a valuable reference work for students of twinning and of cattle genetics. In spite of all the numerical details, the conclusions are not entirely quantitative and some of them seem to be considerably subjective. Perhaps it is better to be somewhat subjective and fairly complete than to be altogether objective but very incomplete. He who would describe an animal or its performance is often faced with something of that choice.

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THE HISTORY OF DOMESTICATION

IN this instructive little book* the author has given a very interesting and plausable presentation of the probable steps involved in the development of our domestic animals from their wild forebears. The causes for the wide diversity of form within most of our domestic species compared to the relatively few forms of the same or related species found in the wild state are discussed. Thus he explains how in large measure domestic animals, natural selection has been replaced by artificial or human selection and how modification, mutation, and recombination of characters have made possible the process of domestication.

A general discussion of the alteration of the "raw material" in the course of domestication is given in Chapter IV, while in Chapter V Professor Nachtsheim presents in considerable detail the course of domestication in the rabbit.

That the process of domestication starting some twelve thousand years ago with the dog is still going on, is pointed out with regard to changes still taking place in the earlier domesticated species. Furthermore it is of interest that new species are even now beginning to be subjected to the process, as in the case of the silver fox and other fur-bearers.

There is an appendix with 16 plates of very apt illustrations.

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U. S. Dept. of Agriculture

*NACHTSHEIM, HANS. Vom Wildtier zum Haustier (from Wild Animal to Domestic Animal). Alfred Metzner Verlag, Berlin. 1936.

AN ORANGE-COLORED BUD SPORT OF THE AGEN PLUM

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MUTANT AND NORMAL AGEN PLUMS
Figure 16

On the left is shown fruit and seed of the orange mutant. On the right, a normal fruit. In characteristics other than fruit color and small size of pits the mutant Agen plum seems identical with the normal form of this old variety.

ON September 17, 1935, the writer observed a branch of an otherwise normal Agen plum (French prune) tree which was bearing fruit of an orange color and displaying other characters sufficiently distinct from those of the remainder of the tree to justify recording it in the list of bud sports of deciduous fruit trees.

The Agen is an old variety of the domestica plum group. It was introduced to this country from Europe and is the most extensively planted plum in the Pacific Coast States. The normal fruit, which is dull reddish-purple in color when mature and black when dried, is used exclusively for prune making. Differences in size of fruit borne by individual trees of this variety and between branches of the same tree have been observed, but bud sports like this one have rarely if ever been recorded before. A yellow-fruited Agen plum sport that is somewhat like the one discussed here was observed by Mr. A. D. Shamel and Mr. C. S. Pomeroy of the U. S. Department of Agriculture, who are stationed at Riverside, California; and so it seems probable that other sports of a similar type are in existence and might be found if sufficient search were made.

The present bud sport originated on a fruiting branch of a bearing tree in the orchard of Mr. J. C. Meischke near Sutter City, California. The tree is about twenty years old; the sporting branch appears to be seven years old and has been observed by Mr. Meischke for several seasons. He stated that he

is positive that no bud or scion has ever been inserted into this tree. The outstanding character of the fruit and the one that brought it to the grower's attention is its orange color. This color, though of a dull tone, contrasts strikingly with the dark reddish-purple of normal Agen plums. When dried it is amber-colored. Other characters that distinguish the sport are the size of fruit and of the pit (Figure 16). The orange-colored sport outranked the normal in size, but the pits from this larger type were smaller than those in the normal red fruit. The average weight of crop samples of tree-ripe fruit for 1935 and 1936 is 27 grams for the orange-colored varient and 23 grams for the normal from branches that are comparably located on the same tree. The length and suture diameter of pits from the orange-colored lots was 20.6 and 11.3 millimeters, respectively, as compared with 22.3 and 12.3 millimeters for the normal.

When the fruit was first examined in 1935, both lots were tree ripe; and the commercial harvest had started. Some of both the red and orange fruit had started to shrivel on the tree, although almost none of either lot had fallen and it was with difficulty that all of it could be shaken from the branches. However, difficulty in shaking ripe Agen prunes from the trees is often experienced in this locality, no difference in the time of maturity or tendency to cling to the branch could be seen between the orange-colored fruit and that on the remainder of the tree in either of the two seasons it has been under observation.

No consistent differences in shape distinguished the orange-colored fruit from that on the remainder of the tree. Both were of the typical Agen type. That from the sporting branch was thought to be a little sweeter than that from other branches of the same tree, but when dried and cooked the two types seemed to be the same in flavor.

The branch bearing orange-colored fruit was much more productive than other branches of the same tree in 1935 and 1937, which were years of good crops. In 1936, a spring frost killed much of the crop on both types of branches. There appeared to be no differences in time of flowering between the sporting branch and the rest of the tree.

The outstanding characters that distinguish the bud sport from the remainder of the tree are the orange color and large size of the fruit, small pits, and heavy production.

Inheritance of Horns and Color in Cattle

In crosses between polled and horned breeds of cattle the offspring are not by any means all polled, even though it is true that the latter condition is due to a dominant gene, and in spite of the fact that the polled parent is homozygous. Some scurred and horned animals usually appear. This can be explained by postulating a gene for scurs (*Sc*) which is epistatic to polled (*P*) in either heterozygous (*Scsc*) or homozygous (*Sc Sc*) males, but which is epistatic only in females which are homozygous (*Sc Sc*). A similar epistatic relation apparently holds for a special horn gene (*Ha*), distinct from the gene (*H*) carried by all horned breeds, and found principally in certain horned breeds of Africa.

A miscroscopic and chemical study has been made of cattle hairs for the purpose of determining the effects produced within the hair by the different color genes. Only two pigments have been found, (1) black, in the form of opaque clumps and granules, and (2) red, nongranular, transparent, and diffused throughout the hair. Various combinations of these two pigments are responsible for all the colored hairs; and the complete absence of the red, together with the almost complete absence of the black, causes the hairs to be white.

Black pigment bleaches more readily with hydrogen peroxide than red. Weak acids have no effect on the pigments, but weak alkalies do have. Eighteen different fat solvents, used singly and in combination, at both low and room temperatures, were found to have no effect on either pigment.—*Dept. of Animal Husbandry—Kansas Expt. Sta.*

A PEDIGREE OF SYNDACTYLY

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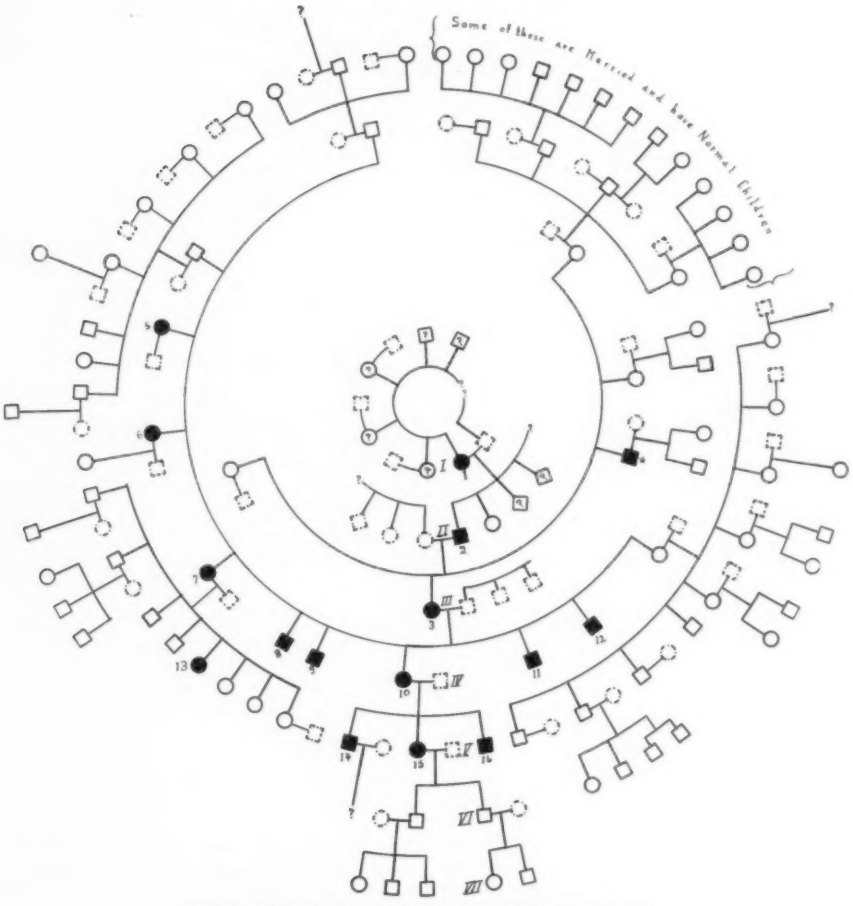
PEDIGREE studies of defects of the extremities in man, such as syndactyly, polydactyly, brachydactyly and other morphological variations, frequently indicate their genetic background by a high familial incidence and by appearing in several successive generations, without displaying a clear-cut conformity to simple Mendelian expectation. Most of them appear to be fundamentally dominant traits, yet show marked irregularities in observed ratios and in the expression of the trait from individual to individual. Some of the suggested causes of these irregularities are unknown environmental influences, instability of the germplasm, genetic influences associated with sex, and incomplete dominance which may be the result of various combinations of modifying factors.

In the case of syndactyly, there is reason to believe that part of this uncertainty in the mode of inheritance is a result of the difficulty in distinguishing between two or more single traits which morphologically resemble each other, but which genetically may be quite different. Thus "syndactyly" is often used as an inclusive term for several of these morphological variations. Weidenreich[13] has suggested the term "zygodactyly" for "webbed digits" as, at least morphologically, distinguished from "syndactyly" which Schultz[11] prefers to limit to skeletal deformities of the hands and feet. The genetic relationships of these possibly different deformities and their mode, or modes, of inheritance can only be established by recording all available data. Of exceptional value are pedigrees showing the inheritance through several generations of any of these variations, alone or in simple combinations.

Information concerning the western New York family here recorded goes back as far as 1800. Nothing is known of the parents of individual I-1, or of the earlier appearance of the trait in this family. Individuals of the fourth generation were interviewed by the writer and willingly supplied the information embodied in this report. Unfortunately, however, they were unwilling to allow photographs or X-ray pictures to be taken.

"Lobster Claw" Type

The deformed individuals are characterized by misshapen and fused bones in both the hands and the feet. In the extreme manifestation, the deformity is like the "lobster claw" reported by Cook,[3] showing a suppression of the central, and an overgrowth of the marginal digits, sometimes resulting in almost complete obliteration of the palm of the hand, and giving the foot a "cloven hoof" appearance. In the less extreme condition, the palm of the hand may be almost normal, yet one of the central digits may be absent or rudimentary, fusion having taken place with one of the lateral digits, which may not show a marked increase in size. The feet seldom if ever approximate the less extreme condition. Moreover, the feet of all deformed individuals are more nearly alike than are the hands. In no case has complete bilateral symmetry of the hands or feet been known. Variation in expression is as great between brother and sister, or between parent and offspring, as between less closely related individuals. It is not as great as the variability reported by Scott,[12] nor is the deformity complicated by polydactyly and simple webbing. The pedigree appears to present a clear-cut case of the type of syndactyly often referred to as "lobster claw." The stock is otherwise normal and healthy, and of average intelligence. From the available information there has been no illegitimacy or intermarriage. This fails to support the suggestions of Edwards,[4] Murphy,[5] and Knox,[6] that syndactyly is associated with



PEDIGREE OF A SYNDACTYLOUS FAMILY

Figure 17

Deformed individuals are represented by solid symbols; normal individuals of the family by symbols with continuous outlines; and unrelated normal individuals who married into the family, or their sibs, by symbols with broken outlines. Where information concerning an individual is incomplete or doubtful, that fact is indicated by a question mark.

alcoholism, low mentality and inbreeding.

By study of the pedigree it is found that there are 16 deformed individuals, of whom 8 are males and 8 females. The deformity has been transmitted by five females and at least one male. No information could be obtained regarding the children of individual V-14, who is living in the western part of the United States. Individual II-2 has transmitted the trait to his son III-4, as well as to his daughter III-3. It is therefore unlikely that the trait is in any way associated with the inheritance of sex, in contrast to "webbed toes" as reported by Castle[1] and Schofield[10]. Furthermore, there seems to be no correlation of degree of deformity with sex.

In completely recorded families where one parent is deformed, there is a total of 14 deformed and 18 normal offspring.

In no family is there a significant deviation from the expected 50-50 ratio, assuming one parent to be heterozygous for a dominant trait. With respect to a very similar deformity, Lewis and Embleton,[7] as well as Pearson,[9] found an excess of abnormals in crosses of normal wtih abnormal.

No Skipped Generations

There has appeared no carrier for the trait who does not show it himself. Of the 58 children recorded in cases where normal segregates have married normal individuals, none of them has been deformed. This outcrossing has involved three and four generations in some cases. Heston[5] assumes a dominant gene for "webbed toes" but postulates modifying factors to explain why, in some cases, the trait skips a generation. In reference to a similar skipping of a generation in the pedigree of syndactyly reported by Scott[12], Cook[3] suggests modifying factors which tend to alter the dominance of a normally dominant gene.

In this pedigree the distribution of the affected and unaffected individuals is in complete harmony with a single factor interpretation, in which this particular type of syndactyly is assumed to be completely dominant to the normal condition. This, however, does not exclude the possibility of important modifying factors. They may be responsible for the variation in expression, but in no case does the presence, or the absence, of these or other modifying factors, suppress the gene completely, or on the other hand, fail to bring it into expression.

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Big Babies and Diabetes

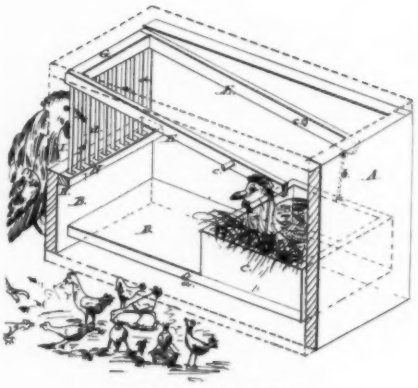
Repeatedly the observation has been noted in medical literature that diabetic mothers have large babies. Joslin has poined out that fat babies born dead suggest examination of the parents for diabetes. Bowcock and McCord have reported an instance of a mother giving birth to babies said to have weighed 12, 15½, 14 pounds, and 12 pounds 2½ ounces (5,443, 7,030, 6,350 and 5,514 Gm.). In her sixth pregnancy, after normal gestation, she bore a baby weighing 12 pounds 2 ounces (5,500 Gm.). In her seventh pregnancy she developed diabetes and, when labor was induced, gave birth to dead twins weighing a little over 3 pounds (1,360 Gm.) each. By the use of insulin and diet she was made sugar free. When she next became pregnant she was kept sugar free without insulin, on a restricted diet, and gave birth at term to a baby weighing 13 pounds 7½ ounces (6,109 Gm.). All the babies were oversize in respect to height and weight.

In a record of large babies born in Great Britain, Dr. W. F. Christie indicates that infants heavier at birth than 10 pounds (4,535 Gm.) may be postmature rather than obese and does not indicate any relationship to possible diabetes. The largest babies born, according to American medical records, include a case described by Dr. D. P. Belcher of a woman who gave birth to a baby girl (stillborn) that weighed 25 pounds (11,340 Gm.). There is also an authentic record of a baby born in Italy weighing 24 9/10 pounds (11,294 Gm.), and Birnbaum discusses the case of a child weighing 11,300 Gm. at birth. — *Jol. Amer. Med. Assoc.*, Nov., 1936.

A TRAP-NEST POSTSCRIPT

DR. GOODALE'S inquiry regarding the origin of the trap-nest inspired a little research in the Patent Office regarding the invention of this useful instrument. The evidence suggests but does not prove that the concept of selective breeding in poultry considerably antedated Gowell's experiment. The "art" (as the Patent Office calls it) of trap-nesting began about the time of the Civil War. In 1866, G. Wolf patented a "cage trap" which could be used for trapnesting fowls, though the text of the patent indicates that he planned to use it as an animal trap. In the next decade many devices were evolved which might have been modified to have been used as trap-nests but in practice were not intended that way. The purpose of all of them is to "provide a nest box, which will close automatically when the hen gets upon her nest, and will open in the same manner when the fowl wishes to leave her nest, whereby a sitting hen may be protected from annoyance from other fowls, or other animals prone to annoy hens while hatching or laying." The poultry-minded inventors of America of that time seem to have been very much wrought up over the psychological and other hazards to which the laying hen was exposed. All of them arranged their devices so that the hen was able to escape either through the action of random events or by the application of varying degrees of avian ingenuity. In 1869 a patent was issued to D. P. Leich for a trap-nest on which no mention is made in the inventor's description of any way in which the hen could escape. This is the first instance found of a trap-nest specifically for poultry which could be used to locate the more fecund members of a flock.

Not until 1899 was a patent issued which made any reasoned statement in regard to the place of the trap-nest in a breeding program. In that year patent No. 621,499 was issued to George



FOILED AGAIN!

Figure 18

Facsimile of illustration from specification of Hayward patent of 1868 showing gravity-actuated door which closes when hen gets on nest, and opens when she gets off. "Devilish ingenious" thinks the rooster, but of no great worth to the breeder. Whether the happy scene in the foreground represents a dream of the hen's, or just fanciful *ad libbing* on the part of the artist does not appear.

I. Lytle which clearly set forth the breeding possibilities of trap nesting. Lytle has this to say about selective breeding in the specification of his patent:

> In the successful and practical culture of poultry the experienced poultryman finds it necessary to keep a proper record not only of the egg-producing capacity of the poultry, but also of the best breeders; and the present invention is primarily designed to assist the poultryman in keeping such record.
>
> It is well understood that in every flock there are barren hens which produce no eggs, but which can only be maintained at the same expense as those hens which are desirable to keep on account of their prolific laying qualities.
>
> The present invention enables the poultryman to readily detect the barren hens, so that the same can be disposed of, as well as to determine the exact egg-producing capacity of each hen, as it is also well known that in a flock there will be found a great difference in the number of eggs laid by different hens, some hens producing two hundred or more eggs a year, while others will only produce fifty eggs a year or even less, and

it is never desirable or profitable to keep the latter class of fowl.

Furthermore, the present invention enables the poultryman to use only his most profitable fowls for breeding purposes and will also enable him to have on record the exact egg-producing capacity of each hen offered for sale, and thereby obviate the necessity of separately penning up "prize" fowl in pens, as has heretofore been the custom.

This patent was filed on October 17, 1898, so that this statement dates from the same year as Gowell's experiment began. Gowell lived in Maine, and Lytle in Wisconsin, so the basic idea of using trap-nests in poultry selection seems to have been quite wide-spread at that time.

The records of the Patent Office also yield another approach to this problem of selective breeding which has not attained any great popularity although the inspired ingenuity displayed does deserve a place in a history of breeding. In 1910 a patent was issued to Stanley A. Merkeley covering a marking and dating device which, attached to the hen, identified her egg by applying a rubber stamp to it as it came into the world. A brief description of this device should be, and herewith is, incorporated into the literature of irrelevant geneticana. It consisted of an elastic ring carrying inking rollers—the whole attached to the vent of the hen by four metal clips, somewhat as a nose-ring is attached to a hog. The inking roller (or rollers) on the elastic ring produced a code of different colored stripes, dots, and dashes, which identified each egg. Fortunately for the comfort of our feathered barnyard friends, the device has not proved to be a best seller. It does, however, represent an ingenious approach to a biological problem even though one which the S.P.C.A. might take exception to.—Ed.

◆

COMPLICATIONS IN EAR GENETICS

In the Journal of Heredity for June, 1937, appears a brief report on "Ear Lobe Inheritance." From the interesting pedigree there presented, the authors conclude that adherent ear lobes are pure recessives in their inheritance to free ear lobes.

In 1931, in the course of some studies on the inheritance of the blood groups (*Jour. Immunology*, vol. 20, p. 371, 1931; *Human Biology*, vol. 5, p. 577, 1933), data were also collected on the inheritance of ear lobes and the method of clasping the hands and folding the arms (*American Naturalist*, vol. 66, p. 365, 1932). Since the data on the inheritance of ear lobes have never been published, it occurred to me that it might be appropriate to present it at the present time.

First, I should point out that the arbitrary classification into two sharply defined types: one with completely attached ear lobes, and the other with completely free ear lobes gives a false picture, since all gradations between the two extremes are encountered. Moreover, in occasional individuals the two ears may exhibit differences, and, in rare instances, one may be free and the other attached. Hence, I found it necessary to classify the individuals into at least four arbitrary groups which I

TABLE I. EAR LOBE INHERITANCE

CROSS	NO. OF FAMILIES	CHILDREN				
		0	1	2	3	Totals
0×0	5	12	2	0	0	14
0×1	7	21	5	10	2	38
1×1	8	80	17	3	1	41
0×2	18	45	19	11	2	77
0×3	9	17	9	12	4	42
1×2	19	33	31	29	4	97
1×3	18	13	15	19	4	51
2×2	24	39	31	47	8	125
2×3	22	20	19	35	17	111
3×3	2	0	2	7	2	11
TOTALS	134	280	150	193	44	607

have designated as 0, 1, 2, and 3, respectively, where 0 corresponds to the completely free ear lobe, 3 to the completely attached ear lobe, and 1 and 2 represent intermediate types. Table I summarizes my findings.

It will be seen that, although there is a definite correlation between the types of ear lobes in the parents and in the children, no simple mechanism of inheritance can be derived. Probably, as with other quantitative differences, more than a single pair of allelomorphic genes is involved, or possibly there is only a single pair of genes, but the effect of these genes is modified by the combined influences of the other genes.

The purpose of this communication, therefore, is to take the occasion offered by the report on "Ear Lobe Inheritance" to present some unpublished data on the inheritance of this trait and also to correct some misconceptions which the reader may possibly derive from reading that report.

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Brooklyn, N. Y.

◆

STABILITY AND INSTABILITY OF SEXUAL CONDITIONS IN MORUS ALBA*

John H. Schaffner

In the spring of 1936, the writer had a considerable number of young white mulberry trees (*Morus alba* L.) coming into bloom. Ten of these trees, ranging in height from 9 to 12 feet, were very carefully studied for their sex expressions and labeled, in order that any possible future changes might be definitely determined. These trees were seedlings four years old and were planted in very rich garden soil. Five of the trees were completely carpellate or female and five were completely staminate or male. There was no indication of inter-sexual expression in any of their catkins.

When these trees bloomed again in 1937, they had increased in size and now ranged from 10 to 14 feet in height. Three of the five trees that were pure female in expression in 1936 were again pure female but two of them showed some sex-reversal, having developed some pure staminate catkins and some mixed catkins, containing both staminate and carpellate flowers, along with the numerous carpellate catkins. Of the five trees that were of pure male expression in 1936, three were still pure staminate, showing no sign of femaleness in any of their catkins, but two had also undergone sex-reversal. One of these two trees was still decidedly male, but had a few carpellate catkins among the numerous staminate catkins. The other tree had changed to extreme femaleness, having large numbers of carpellate catkins, which later produced abundant fruit, and only a very few staminate catkins. Had the previous history of this tree not been known it would have been regarded as a carpellate tree with the slightest indication of sex-reversal to maleness. Some of the carpellate catkins were small and short, sometimes with not more than six flowers. The great majority of the catkins, however, were normal in size and both the large and small catkins developed into fruits. At maturity this tree appeared as abundantly fruitful as any of the trees which had been carpellate originally and had remained so.

This change from a pure male condition to a nearly pure female condition took place in a single year and apparently without any outside influ-

*Papers from the Department of Botany, The Ohio State University, No. 393.

ence except that the trees had been subjected to rather severe drought conditions when young, while the past year has shown a decided advance in the amount of precipitation. The sex of many white mulberry trees is apparently constant for indefinite periods, but that they can undergo extreme sex-reversal under proper ecological-physiological conditions is shown by the present cases and many previous observations. It is plainly evident that the myriads of cells which reversed their sexual states in the vegetative buds within the period of twelve months or less did so entirely through physiological changes and not through any hereditary mutation or loss of either entire chromosomes or individual genosomes.

In recent years some botanists have attempted to analyze the sexual nature of various species of plants by hybridizing supposedly different hereditary sexual strains or varieties and observing the sexual nature of the progeny appearing at the first reproductive period. Such a procedure can give no conclusive evidence for determining the actual sexual nature of either the individual or the race. The plants showing a certain sexual character at their first blooming period may develop the opposite sexual state at a subsequent reproductive period. The true genetic constitution in relation to sex potentialities can only be determined by observation and experiment on the individual for many reproductive or growth periods under a large assortment of ecological conditions. The sex label attached to an individual of very many dioecious species at any reproductive period can only describe the character of the individual for the time being.

In addition to the phenomena of reversing sexual expressions, there are also somewhat similar phenomena produced by potentialities which give sporadically recurrent or intermittent hereditary vegetative characters, as the production of spiral sheaths in an individual which usually produces cyclic sheaths or the lack of internodal development in a zone of a shoot which usually has prominent internodes throughout its entire length. It has been definitely established that such changes of character expression occur without any change in the hereditary structure or constitution of the tissues involved and are not to be confused with actual vegetative mutations. Such sporadically recurrent characters are common in species of Equisetum and other plants and indicate that the actual, hereditary, potential system, whether involving sexual or vegetative characters, can only be determined by a study of the plant in all of its possible physiological and morphological reactions.

7TH INTERNATIONAL CONGRESS OF GENETICS

To Be Held in Edinburgh

In accordance with a resolution of the International Committee and with the decision of the Organizing Committee elected by the Genetical Society of Great Britain, the 7th International Congress of Genetics will meet in Edinburgh in 1939, probably from August 23rd-30th inclusive. Professor F. A. E. Crew, Institute of Animal Genetics, University of Edinburgh, Edinburgh, 9, has been appointed General Secretary to the Congress and to him all correspondence concerning it should be addressed.

THE PROBLEM OF RACE BETTERMENT*

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MAN has long recognized the need for a definite program leading to the betterment of the human race. The Greek poet, Theognis, called attention to the fact that whenever man seeks a sire for animals he chooses only those possessing desirable characters but this choice of a husband for a daughter is often influenced by the wealth of the suitor. Plato suggested that the State assume control of human matings, thereby fostering the propagation of those considered best and the prevention of the birth of those deemed detrimental to society. Aristotle visualized the problem as one that was closely allied to social and economic problems and could be corrected through their adjustment. The first scientific approach to an understanding of the factors in human inheritance was made by Francis Galton in 1865 and his work culminated in the development of the science of Eugenics whose objective is to point out the road leading to race betterment.

Evidence shows that the United States cannot afford to ignore this question, for the human race depends for its supremacy over animal life upon man's mental ability. Many animals surpass man in strength, speed or cunning, yet by virtue of his powers of thought he can dominate and control all. Destroy this power and you destroy man. Yet approximately 300,000 mental patients are confined in institutions today and it is not an exaggeration to state that an equal or greater number are never brought to the attention of the statistician. Reliable estimates have placed the number of mental defectives in this country as approximately ten per cent of the total population. These defectives are not decreasing in numbers as might be expected where the biological law of the survival of the fit has had full play, for the increasing belief of the brotherhood of man has permitted defectives to be perpetuated and even has had the effect of encouraging their increase. Defectives can in no way be a benefit to civilization, for not only are they unable to appreciate the problems of national existence but rest as a burden upon the normal individuals. To provide for these defectives hospitals and asylums must be maintained, police forces must be adequate and prisons sustained. It is the individuals of low mentality who compose close to seventy-five per cent of the social offenders. These, like animals think only in terms of the present and respond to immediate needs without thought of future discomforts and the rights of others.

Even after realizing that there exists malignant human infections in civilization, difficulties arise in their identification and removal. These obstructions may be grouped as emotional, factual, legal and ignorance.

Obstructions

Emotional obstructions are always at the beginning and end of any progressive movement. There are various "taboos" regarding any discussion that has any reference to the important question of reproduction. Behind this the defectives seek refuge fearful that the study of their family will draw forth the family skeleton, or possibly feeling with Robert Burns that their *ancient and ignoble blood has crept through scoundrels ever since the flood.*

Emotional taboos obstruct the collection of factual knowledge regarding the

*Presidential address given before the Knoxville Science Club, May 28, 1937.

manner by which specific human traits are inherited and since the exact knowledge of the mechanism of inheritance is only recent, an understanding of the manner by which human traits are inherited will require the full cooperation of all. The span of man's life is long, his development slow and involved, his offspring few and the selection of a mate consists of each individual choosing the one that comes nearest to his or her common ideals. Even if possible, experimental breeding is impractical. Thus the collection of specific facts is hindered and recourse must be found to records of inmates of institutions, for tombstones tell little of the really essential facts regarding dead ancestors.

In spite of the difficulties confronting the understanding of human characters certain traits have been found to follow the laws of inheritance as established by animal experimentation. Characters like polydactylism, congenital cataract and Huntington's chorea behave as dominants and approximately half of the offspring show the defect. Characters like feeble-mindedness and deaf-mutism resemble recessive traits which are not expressed unless brought in by both parents. Interesting sex-linked characters like color blindness, haemophilia, etc., make their appearance usually only in the male line and are passed on to the daughters and by them to their sons.

Inheritance Not Simple

There is no disputing the inheritance of these characters: the evidence for their Mendelian inheritance is proven but man is not a simple organism, many characters for which we have come to use one term involve the transfer of many genetical units as well as being subject to environment. In no way can "ability" be thought of as a simple human trait. Ability in art is dependent upon seeing, muscular control, training and experience. To attempt to treat such a character as a simple Mendelian unit can only be excused on the basis of ignorance. Any attempt to do this is apt to throw question on the significance of heredity in respect to all characters, for a skilled environmentalist can show such a character the result of environment with equal conviction. Such, however, is not possible when simpler dominant, recessive or sex-linked characters are considered. These show their conformity to the genetical laws.

Incompleteness of factual knowledge leads to legal difficulties and not having crystalized evidence permits those enjoying advantages under the present system to raise high the cry of the encroachment of personal or religious liberties. The reactionaries have long found it expedient to appeal to a true principle to support false doctrines or selfish gains, and any program for race betterment meets with the same opposition.

Lastly in the path of any constructive eugenic movement is the "laissez-faire" attitude strongly supported by ignorance of heredity, ignorance of the need of race betterment and a failure to develop a eugenic consciousness of individual responsibility.

Laws

Any eugenic program is closely linked with economic, legal and social conditions. Aristotle recognized the need for economic adjustment which would afford equal opportunities to all and special privileges to none. He saw the need of the utilization of all natural resources wherever needed by those best capable of their full utilization. Unobstructed competition must be assured so as to eliminate the inefficient. Unfair competition, however, due to legal monopolies must be prevented for they will destroy the strong and permit the perpetuation of the privileged. It is essential to guard against all forms of special privilege for like a mutation in the animal kingdom, once established, no matter how slight, it will be gradually increased until it controls all or falls by its own weight. A just state can only be maintained in accordance to democratic principles and the biological law of the survival of the fit.

Certain legal aids are desirable for the fulfillment of a sound eugenic program. Among these is the maintenance of institutions and prisons for the segregation of violators of social and moral customs which have been embodied in legal statutes. Supplementing these restrictive measures, it might be desirable to have laws permitting the sterilization of individuals whose offspring would obviously be a burden upon humanity, for the argument once so loudly voiced as to the dire effects, has faded into a myth with the putting of these measures into practice. Immigration laws should be maintained, not to restrict the good blood of foreign lands but to prevent the inflow of emigrants which tend to settle into distinct colonies equivalent to the establishment of a miniature foreign land within our borders. In these localized centers of foreign thought, American ideals, customs and policies can filter in only very slowly and from them emanates alien thoughts, ideals and customs.

Marriage legislation has distinct value as it touches most immediately the problem of race betterment. A healthy race cannot be built from marriages between the unhealthy. "Whim" marriages are not to be condoned for too frequently such are followed by the addition of a new individual to the world and upon these individuals the future of the race depends. The saving of a squire's fee, is like the selling of a nation's birthright for a mess of pottage. Nor are child marriages desirable, for although biologically both parties may be mature, they bring into the world citizens which like their parents will have neither the opportunity nor possibly the ability to develop into the type of individual necessary for a successful race.

The hope of the eugenic movement rests in the development, on the part of all, of a strong genetic consciousness of responsibility for the race. This must be based upon a knowledge of inheritance as well as the realization of the needs of race betterment. There must be an appeal to race survival, culminating in a race consciousness so strong that men and women will respond genetically to protect their race and ideals with the same vigor as they respond to an invading army. There must be a realization that even more powerful than an invading force is the inherent undermining of a civilization by its defectives.

War itself is eugenically unsound, for it destroys the thing men are fighting to preserve. It is the higher type of individual who first responds to the call to defend a nation at the risk of possible self sacrifice. Yet with the death of such a man, the weak and the selfish remain to propagate individuals who have no conception of the ideals for which the hero died. Truly, man is a fighting animal, he has gained his supremacy through fighting, but modern war has reversed the conditions, for the strong are now destroyed and the weak survive. Man can never hope to eliminate war but he can hope to substitute economic warfare for physical strife.

Man has intelligence, he alone can look into the future, he alone can understand and interpret natural laws and by his intelligence he may direct not only the development of animals but his own destiny. Through his intelligence and through the development of a eugenic interest he may raise the conception of the perfect man and as each individual selects a mate with knowledge and reason, the nation will progress to an ever higher type of civilization and one which in its ultimate development, can never be destroyed.

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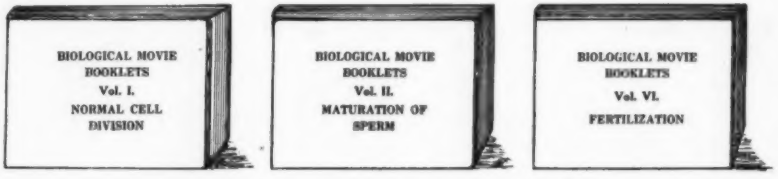

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